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THE CEPHALASPIDS OF GREAT BRITAIN

BRITISH MUSEUM
NATURAL HISTORY

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BRITISH MUSEUM (NATURAL HISTORY)

THE CEPHALASPIDS OF GREAT BRITAIN

BY

ERIK ANDERSSON STENSIÖ

WITH SIXTY-SIX PLATES AND SEVENTY TEXT-FIGURES

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PREFACE

In this British Museum Catalogue the results of Professor STENSIÖ's most recent work are embodied as an anatomic and systematic treatise. Professor STENSIÖ is well known as the highest authority on those early vertebrates allied to Recent lampreys and known as Cephalaspids. His marvellous technique may be said to have revolutionized our methods of research, revealing, as it does, detail which enables even certain soft parts to be so reconstructed that our knowledge of these ancient fossils is in some respects almost as complete as that of Recent forms; and his skill in evolving this technique has only been equalled by the patience needed to carry out his elaborate dissections.

Moreover, Professor STENSIÖ's latest researches are appropriately published here; for most of the known specimens of British Cephalaspids, totalling about three hundred, and about half of the type-material figured in this volume, form part of the British Museum Collection. Further, these researches supplement Professor STENSIÖ's earlier work on the Cephalaspids of Spitsbergen; for, while the head-parts of those are known in great detail, especially the nervous and vascular systems, their bodies and limbs are almost unknown; whereas the British forms, while generally showing well-preserved head, body and limbs, yet do not present on the whole the wonderfully well-preserved details of head-structure exhibited by the specimens from Spitsbergen.

In common with his former works, this monograph is illustrated by photographs taken by Professor STENSIÖ himself, and a glance at the plates, and still more, comparison of the plates with the actual specimens, will indicate the remarkable quality of the original prints.

In addition to those whose scientific help the author has duly acknowledged, I should like to thank the following for supplying information and material: Mr. W. WICKHAM KING, on whose information the chapter on the stratigraphical relations of the fauna is entirely based; who has also generously presented to the Museum all those specimens of his collection figured in this work; Dr. P. H. GRIMSHAW, Keeper of the Natural History Department of the Royal Scottish Museum, Edinburgh, for providing details of localities and collectors of the remarkable series of specimens under his charge; Professor E. STROMER VON REICHENBACH, of Munich; Dr. WERNER QUENSTEDT, of Berlin; Dr. J. GILES LANG, of Ludlow Museum; Mr. A. G. BRIGHTON, Curator of the Sedgwick Museum, Cambridge; Professor W. J. SOLLAS, of Oxford; and Dr. C. J. STUBBLEFIELD, of H. M. Geological Survey; for similar aid. I should also like to express my appreciation of the public spirit shown by the Committees of the Museums at Hereford and Dundee, who, thanks to the hearty co-operation of their respective Curators, Mr. F. C. MORGAN and Mr. A. S. WEBSTER, have readily agreed to exchange with the British Museum some of the valuable Cephalaspid material in their Museums, thus adding greatly to the richness of the National Collection.

Great credit is due to my colleague Dr. E. I. WHITE, who has relieved Professor STENSIÖ of the laborious task of editing the type-script and seeing the whole through the press. He has been helped by Mr. H. A. TOOMBS, of the Geological Department, who, especially, has been responsible for the index.

* * * * * * * *

The Cephalaspids are among the most important and interesting of vertebrate fossils because of their great antiquity and the light they throw upon the evolution of vertebrates. The material is often well preserved, and always valuable; for these fossils, at no time very plentiful, are now rarely found, since of their chief sources, the railway-cuttings and the road-stone quarries, the former are now inaccessible and the latter mostly abandoned. These sections were cut either in the Old Red Sandstone or the passage-beds between that formation and the underlying Silurian. The term "Passage-Beds," written on the original labels of many of the specimens, is quoted as "Downtonian" in the Systematic Description and Explanation of Plates; otherwise the information on the original labels is recorded as written. But some of the specimens were collected more than a century ago, and many before collectors appreciated the value of recording the provenance exactly; indeed labels on old specimens are known to have been made intentionally vague so as to preserve the finder's monopoly of a favourable locality. Nevertheless, in most cases it has been possible to correlate the original information with modern stratigraphical knowledge, and this correlation is given in the Chapter on "Distribution."

W. D. LANG.

Department of Geology,
British Museum (Natural History).
15*th June,* 1932.

AUTHOR'S PREFACE

THIS work on the British Cephalaspids is based on material belonging to the following museums and collections: the British Museum (Natural History), London; the Museum of Practical Geology, London; the Royal Scottish Museum, Edinburgh; the Museum of the Albert Institute, Dundee; the Hereford Museum; the Ludlow Museum; the University Museum, Oxford; the Sedgwick Museum, Cambridge; the University Museum, Birmingham; the Geologisch-Palaeontologisches Institut of the University of Tübingen; the Bayerische Sammlung für Paläontologie und historische Geologie, Munich; the Museum für Naturkunde, Berlin; and the collection of Mr. W. WICKHAM KING, of Winds Point, Hagley. To the authorities of these museums and to Mr. KING I wish here to express my deepest gratitude for the courteous way in which they submitted their extremely valuable material to me for study. I also wish to offer my most sincere thanks to Sir A. SMITH WOODWARD for his kindness in placing at my disposal his unpublished MS. on the Ostracoderms, which he had prepared for a supplement to his "Catalogue of the Fossil Fishes in the British Museum": this MS. has been a great help to me.

To Dr. ERROL I. WHITE, of the British Museum (Natural History), I am specially indebted, not only for much help during visits to London in 1927 and 1929 for the examination of certain type-specimens, but also for what he has done to facilitate my studies of the British Museum material. I wish also to thank Dr. WHITE cordially for the help he has given me in providing a list of the local English and Scottish Museums in which remains of Cephalaspids are preserved. Also to the late Professor J. KIAER, of Oslo, my most sincere thanks are due for the interest he took in this work and for the valuable information I received from him as to material of Cephalaspids in English museums.

Finally, it is a great pleasure to acknowledge here my debt of gratitude to the following gentlemen who have placed material at my disposal and in other ways facilitated my studies for this work: Dr. F. A. BATHER, London; Dr. W. D. LANG, London; Sir J. S. FLETT, London; Professor D. M. S. WATSON, London; Dr. J. RITCHIE, Edinburgh; Professor W. J. SOLLAS, Oxford; Mr. F. C. MORGAN, Hereford; Dr. J. G. LANG, Ludlow; Dr. H. WOODS, Cambridge; Dr. L. J. WILLS, Birmingham; Mr. A. S. WEBSTER, Dundee; Professor Dr. F. BROILI and Professor E. STROMER, Munich; Professor Dr. E. HENNIG and Dr. H. ALDINGER, Tübingen; and the late Professor Dr. J. F. POMPECKJ, Berlin.

E. A:SON STENSIÖ.

Riksmuseets Paleozoologiska Avd.,
Stockholm.
May, 1931.

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HISTORICAL

CEPHALASPID remains from England and Scotland were first described by AGASSIZ in 1835 (pp. 135–147; see also 1844*b*, p. 307). These remains had been placed at AGASSIZ' disposal by JAMESON, LYELL and MURCHISON. In his "Silurian System" MURCHISON (1839, pp. 587–592) gave an account of the discovery of vertebrates in the Old Red deposits of England and Scotland, followed by descriptions of the British Cephalaspids quoted principally from AGASSIZ. In the same work MURCHISON (pp. 605–607) also published a short notice by AGASSIZ on *Sclerodus* [*Eukeraspis*], which, as we know, proved later to be a Cephalaspid (*cf.* the description of the genus *Sclerodus*). General remarks on the material described by AGASSIZ in 1835 were published afterwards by HUGH MILLER (1841, pp. 136–145), by AGASSIZ himself (1844*a*, pp. 5, 31) and by certain other writers. In 1857 several new British species of Cephalaspids were described by EGERTON (pp. 282–289), and this paper was followed by descriptions of new British Cephalaspid material by HARLEY in 1859 (pp. 503–505), POWRIE in 1861 (pp. 137–141), LANKESTER in 1867 (pp. 152–154) and SALTER in 1869 (p. 240). In 1870 the monograph on the British Cephalaspids by LANKESTER appeared, and with this our knowledge of the Cephalaspids was greatly increased. In this monograph LANKESTER gave good descriptions and drawings of all the material of British Cephalaspids known at that time; in all he described no less than 13 species, several of which were new to science, and he also discussed the systematic position and relationships of the group. Until quite recently this monograph of LANKESTER'S remained one of the most important contributions to our knowledge of the Cephalaspids.

After LANKESTER'S work nothing new was published on the British Cephalaspids until 1891, when Part II of WOODWARD'S "Catalogue of the Fossil Fishes in the British Museum" appeared. In this publication WOODWARD undertook a revision of all the genera and species then known; but he did not confine himself to this, for he gave also a more complete account of the structure of certain species than had been done by earlier writers, especially important observations being made on *Hemicyclaspis murchisoni*, of which new and very well preserved material had been discovered since 1870. Finally, new material of British Cephalaspids has also been dealt with by TRAQUAIR (1893, pp. 206–207; 1894, pp. 269–273; 1899*a*, pp. 591–593; 1899*b*, pp. 834–837, 857–858; 1905, pp. 883–886), who described the new and highly interesting genus *Ateleaspis* (1899*b*, pp. 834–837; 1905, pp. 883–886).

General and anatomical accounts of British Cephalaspids have been published by HUXLEY (1858, pp. 270–273, 277–280), PATTEN (1903*a*, pp. 827–859) and WOODWARD (1898, pp. 8–12; 1921, pp. 31–33). Smaller contributions to our knowledge of the British Cephalaspids are also found in the papers and works of several writers, as for instance in WOODWARD's paper "The Study of Fossil Fishes" (1906, pp. 267–270), in JAEKEL's paper "Über *Tremataspis* und PATTEN's Ableitung der Wirbeltiere von Arthropoden" (1903, pp. 84–93, text-figs. 3, 4), in GOODRICH's "Vertebrata Craniata" (1909, in LANKESTER's "A Treatise on Zoology": Part IX, pp. 200–204) and in STROMER's "Lehrbuch der Palaeozoologie" (1912, pp. 38–39, text-fig. 50), etc.

For the history of the Cephalaspids in general the reader is referred to my monograph on the Spitsbergen Cephalaspids (STENSIÖ, 1927). In that monograph the different opinions advanced concerning the relationships of the Cephalaspids are also dealt with in detail.

DESCRIPTION OF THE BRITISH CEPHALASPID FAUNA

MATERIAL AND METHODS

THE material of British Cephalaspids studied for this work is considerable, and consists both of specimens complete with cephalic shield and trunk and of detached skeletal remains.

The rocks in which the British Cephalaspids occur are generally sandstones or conglomerates of various colours: light grey, grey-red, red, yellow-brown, grey-green or blackish. The skeletal remains found in the light-grey, grey-red or red rocks are as a rule whitish or bluish-white, whereas those in the others are, with few exceptions, almost black.

The exoskeleton is in such a good state of preservation in most specimens that I have been able to study it in much greater detail than in the Spitsbergen forms. The endoskeleton, on the contrary, has been found preserved in only a few specimens, and even in these it is so imperfect that only a few details could be elucidated.

The preparations were mostly carried out by hand under binocular microscopes. In a few cases nitric acid was used, and by this beautiful impressions of the external surface of the exoskeleton with ornamentation and other superficial markings (Pl. 22, fig. 6) were obtained: this method, however, could be employed only when the specimens, usually blackish, were in a matrix which acid would not attack. The grinding method invented by SOLLAS (1903) has not been employed for this work.

In several cases the finest details could not be prepared or studied until the specimens were coated with, or immersed in, certain fluids, such as thick Canada balsam, Canada balsam diluted with xylol, xylol, eugenol, alcohol, oleum cedri, etc. In the case of specimens of a whitish or bluish-white colour, thick Canada balsam was the only fluid which gave the desired results, but with specimens of a black-brown or black colour, diluted Canada balsam, xylol, eugenol and alcohol were all satisfactory. For the preparation or study of details of specimens immersed in diluted Canada balsam, xylol, eugenol or alcohol it was necessary, however, to use specially strong lamps to obtain sufficient illumination. The lamps employed for this purpose were: the " Monla " lamp, manufactured by Leitz; the big micro-lamp, manufactured by Reichert; and the " Pointolite " lamp, manufactured by Reichert.

Many specimens, as noted below in the explanation of plates, were photographed in either thick or diluted Canada balsam. In this way it was possible to obtain pictures much richer in detail than would otherwise have been possible.

ANATOMY

GENERAL REMARKS ON THE CEPHALIC SHIELD[1]

External characters of the cephalic shield.—A distinct cephalic shield is known to be present in all British Cephalaspids except *Ateleaspis*, and it is very likely that it was also present in *Ateleaspis*, although, on account of the imperfect state of preservation of the material, no such shield is clearly discernible in that genus. In general proportions the cephalic shield exhibits a fair range of variation in the different genera and species.

As in the Spitsbergen forms the cephalic shield comprises a cephalic division and an abdominal division.

The cephalic division is always well developed and agrees in all essential characters with that of the Spitsbergen forms. The rostral margin may be either angular or rounded, while in *Cephalaspis acutirostris* (text-fig. 32; Pl. 40, fig. 3) there is a short rostral process, very much as in *C. campbelltonensis* or *Hoelaspis angulata* (Stensiö 1927, text-fig. 77; Pls. 44, 45).

Both in position and shape the orbital openings are as in the Spitsbergen forms, and like them each is surrounded by a thickened and somewhat raised border. This border, which is formed exclusively by the exoskeleton, was termed by Lankester (1870, p. 37) "orbital ring" and by Woodward (1891, p. 178) "orbital rim." In this work, however, it will be referred to as the "circum-orbital ridge."

The naso-hypophysial opening consists of the usual three divisions lying in a distinct circum-nasal fossa especially well developed in *Thyestes* and *Didymaspis* (*f.cn*, text-figs. 1, 23, 29A, 42A, 60–62; Pl. 51, fig. 2; Pl. 52, fig. 3). Its posterior oval division (na_2), which is the real nasal opening, is not as a rule, however, situated at the very bottom of the circum-nasal fossa, but on a small elevation: and it is now beyond question that this was so in almost all typical Cephalaspids.

A pineal canal, which perforates the inter-orbital wall and opens on to the dorsal surface of the cephalic division of the shield, is found in all the British Cephalaspids, just as in those from Spitsbergen. From the cranial cavity the pineal canal ascends more or less vertically through the endocranial roof of the cavum cerebrale cranii to a transverse depression situated on the dorsal surface of the inter-orbital wall and reaching from one orbital opening across the inter-orbital wall to the other. More exactly, this depression, which may be termed the *pineal depression* (*pd*, Pl. 13, fig. 2; Pl. 18, figs. 2, 3; Pl. 19, figs. 2, 4; Pls. 61, 62), lies slightly behind the posterior division of the naso-hypophysial opening and immediately in front of the dorsal electric field, and its ventral boundary is formed exclusively by the endoskeletal component of the cephalic shield. The pineal depression is occupied by an independent pineal plate of exoskeletal origin (*Ppl*, text-fig. 1; Pl. 1, figs. 1–3; Pl. 7, fig. 4; Pl. 43, fig. 2), which is perforated in the centre by a pineal foramen (*pin*$_2$, text-fig. 1; Pl. 1, figs. 1–3), directly above the pineal foramen situated at the bottom of the pineal depression (*pin*$_1$, Pl. 13, fig. 2; Pl. 15, figs. 2, 3; Pl. 47, fig. 2; Pls. 61, 62), showing that the pineal canal continues dorsally through the pineal plate. The pineal plate is of the same shape as the pineal depression which it completely fills. On its lower surface it has on each side of the pineal foramen a pronounced groove (*gr*, text-fig. 1; Pl. 1, fig. 3) which traverses its breadth. When the plate is in position in the pineal depression (text-fig. 1) these grooves are, of course, closed by the floor of that depression, forming a pair of canals running one on each side from the pineal foramen laterally to the orbital cavity. What function these canals had it is difficult to say, but it is not impossible that they enclosed a vein which drained the pineal organ and perhaps also the most anterior part of the dorsal electric field.

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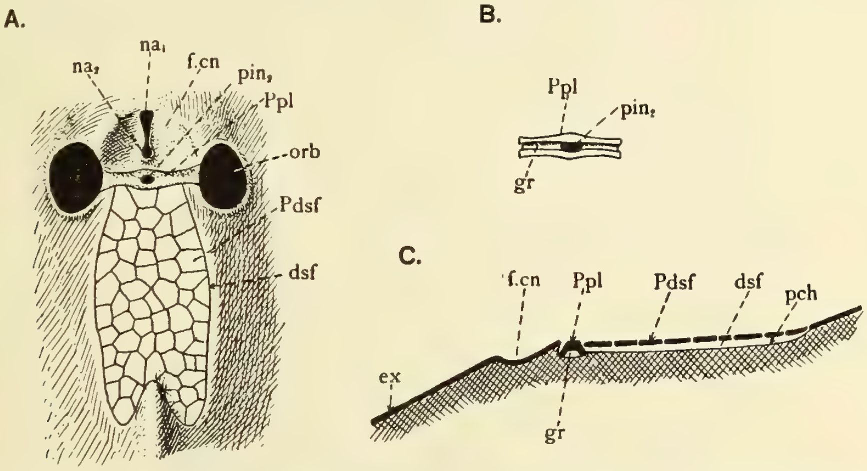
[1] For explanation of the terminology employed in this paper see Stensiö 1927, "The Downtonian and Devonian Vertebrates of Spitsbergen," Part I. Fam. Cephalaspidae.



Text-fig. 1.—Pineal plate of a Cephalaspid showing its position relative to the cephalic shield.

A, dorso-median part of cephalic shield with pineal plate in position; B, pineal plate in ventral view; C, diagrammatic longitudinal section somewhat laterally to the median line of the cephalic shield. The section shows the pineal plate in position in the pineal depression.

dsf, dorsal electric field; *ex*, exoskeleton (denoted by thick black lines); *f.cn*, circum-nasal fossa; *gr*, groove on ventral surface of pineal plate; *na*$_1$, anterior division of naso-hypophysial aperture (opening of hypophysial sac); *na*$_2$, posterior division of hypophysial aperture (opening of olfactory organ, nasal opening proper); *orb*, orbital opening; *pch*, perichondrial bone-layer lining bottom of dorsal electric field; *Pdsf*, exoskeletal plates covering dorsal electric field; *pin*$_2$, pineal opening in pineal plate; *Ppl*, pineal plate.

In the Spitsbergen forms the pineal plate was not preserved, but there was sufficient evidence to prove that this plate was present in them also. It seems clear, therefore, that such a plate was developed generally in the Cephalaspids.

Both the unpaired dorsal electric field and the paired lateral electric fields are present in the British Cephalaspids, and are, on the whole, as in the Spitsbergen forms. In *Didymaspis*, *Sclerodus* [*Eukeraspis*] and *Thyestes*, however, they are shorter than is normal for Cephalaspids. The exoskeletal plates covering the electric fields are found in a good state of preservation in several species, and it has now been possible to ascertain that they consist of the three layers typically present elsewhere in the exoskeleton (*cf.* the chapter below on the micro-structure of the exoskeleton). As is seen in *Hemicyclaspis murchisoni* (text-figs. 1, 15, 23; Pl. 1, figs. 1–3; Pl. 2, figs. 1, 4; Pl. 3, figs. 1, 4; Pl. 4, fig. 2; Pl. 5, figs. 3–6; Pl. 7, fig. 4), *Cephalaspis lankesteri* (text-fig. 41; Pl. 17, fig. 2), *C. pagei* (text-fig. 33A; Pl. 36, figs. 3, 4; Pl. 37, fig. 3; Pl. 38, fig. 4; Pl. 39, figs. 1, 2; Pl. 40, fig. 1; Pl. 43, fig. 1), *C. powriei* var. *brevicornis* (Pl. 28, fig. 3; Pl. 43, fig. 2) and *C. powriei* var. *asper* (Pl. 30, figs. 1, 3; Pl. 31), these plates are subject to certain variations both in number and shape, not only in different species, but also in different specimens of the same species.

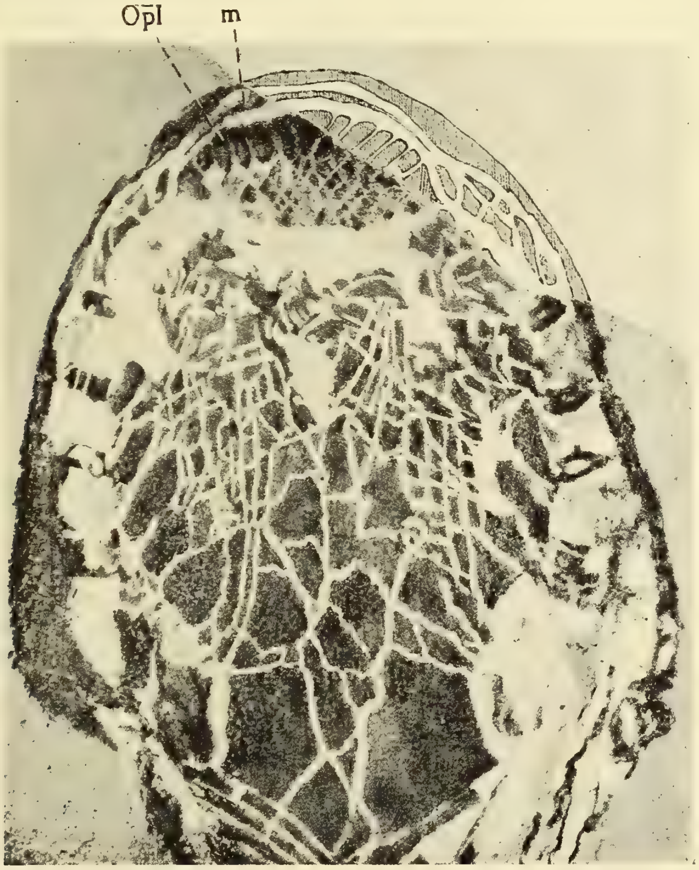
In *Sclerodus* [*Eukeraspis*] the marginal area of both sides of the cephalic division of the head-shield, flanking the lateral electric field and the succeeding abdominal division of the shield, is perforated by four big fenestrae which open on to the ventral rim laterally to the oralo-branchial fenestra (*for_1–for_4*, text-fig. 62; Pl. 52, figs. 1, 2; Pl. 53, fig. 5). From their position and relations to neighbouring organs it is evident that these four fenestrae had nothing at all to do with either the oralo-branchial chamber and the gills, or the lateral electric fields. They were observed by LANKESTER as long ago as 1870 (p. 58), but he believed that they were six in number, and was unable to perceive their true nature; nor have subsequent writers realized that they were merely perforations through the extreme ventro-lateral part of the cephalic shield. Even in 1927 I suggested that together they represented the lateral electric fields (STENSIÖ 1927, p. 24), but from what is now known it seems most likely that their sole function was to lighten the shield.

The ventral side of the cephalic division of the shield can be studied in several of the British specimens, and in all essentials it is as in the Spitsbergen forms.

In the description of the Spitsbergen material it was pointed out (STENSIÖ 1927, pp. 20–21) that the soft tissue that closed the oralo-branchial fenestra was protected on the outside by an exoskeleton of numerous plates. This exoskeleton, for which the term *ventral visceral exoskeleton* is here introduced, has been found preserved among the British forms in *Hemicyclaspis murchisoni*, *Cephalaspis pagei* and *Thyestes egertoni*. In *H. murchisoni*, in which it is best known (text-fig. 8; Pl. 6, figs. 1–3; Pl. 7, fig. 3), it consists in its hinder part of fairly large, irregularly polygonal plates, which pass anteriorly and medially into small, almost rhombic plates in the region just behind the mouth-opening; but the most anterior plates forming the actual posterior boundary of the mouth-opening are so far entirely unknown. In *Cephalaspis pagei* and *Thyestes egertoni* (*vv.es*, Pl. 51, fig. 4) the ventral visceral exoskeleton is very imperfectly known, but nevertheless everything seems to show that in both these species it was very largely as in *H. murchisoni*.

Besides the British forms just dealt with, the ventral visceral exoskeleton is also known in *Micraspis gracilis* and *Aceraspis robusta*, from the Downtonian of Norway, and in *Cephalaspis staxrudi*, from the Downtonian of Spitsbergen. In *Micraspis gracilis* (text-fig. 2), in which it is almost completely preserved, it is fundamentally as in *H. murchisoni*, although its plates are larger and fewer in number. In *Aceraspis robusta* it is said by KIAER (1928, p. 124) to be represented by small *Theolodus*-like scales only. In *C. staxrudi* it is very imperfectly known, but it is clear that it was there composed of numerous small plates. Thus, from its development in both the British and Norwegian forms it is obvious that the ventral visceral exoskeleton is of essentially the same type in all Cephalaspids. In this connection it may be noted that its development is similar in *Tremataspis*.

The relations of the plates of the ventral visceral exoskeleton to the external branchial openings is difficult to ascertain, but judging from what we know, it seems most likely that they did not cover these openings but left them open in the way shown in text-fig. 8.



TEXT-FIG. 2.—*Micraspis gracilis* KIAER. Ventral visceral exoskeleton. Right anterior part restored. × 4 diam. (After KIAER 1928.)
Opl, oral plates; *M,* mouth-opening.

A more detailed account of the ventral visceral exoskeleton is given below in the account of the visceral skeleton.

After the general description of the cephalic division given here we turn to the abdominal or trunk division. As in the Spitsbergen forms, we may distinguish in the latter division an unpaired inter-zonal part and a paired shoulder-girdle or zonal part.

The inter-zonal part varies much in length in different genera and species. Thus it is fairly, sometimes very, short in *Hemicyclaspis*, *Sclerodus* [*Eukeraspis*] and most of the species of *Cephalaspis* (text-figs. 8, 15, 23, 29–31, 35–41, 43–48, 62); fairly long in *Cephalaspis agassizi, C. woodwardi* and the species of *Benneviaspis, Securiaspis* and *Thyestes* [*Auchenaspis*] (text-figs. 42, 50, 55–60); and very long in *Didymaspis* (text-fig. 61). In *Didymaspis* it is longer than in *Kiaeraspis* (Stensiö 1927, text-figs. 3–5), its length even exceeding that of the cephalic division, and in this and most other respects it very much resembles the inter-zonal part in *Tremataspis* (Patten 1903*b*, Pl. 2, figs. 8, 9). Except in *Hemicyclaspis* the inter-zonal exoskeleton is, as far as we know, complete ventrally, *i.e.* its right and left halves meet and are continuous with each other below. In *Hemicyclaspis,* however, there is a wide gap between its two halves ventrally, a gap which is occupied by a great number of small independent exoskeletal plates (text-figs. 8, 24; Pl. 6, figs. 1–3; Pl. 7, figs. 3, 5; Pl. 8, fig. 4) which are continued forwards by the plates of the ventral visceral exoskeleton, backwards by the ventral scales of the trunk. These exoskeletal plates have a rather irregular arrangement medially and anteriorly, whereas laterally and posteriorly they lie in three, more or less distinct, obliquely transverse rows, resembling the rows of trunk-scales following immediately behind them. The boundary between these plates and the ventral margins of the inter-zonal exoskeleton on each side is such that it seems certain that a number of the plates have fused with each half of the exoskeleton, forming a fairly gradual transition between them. Judging by the breadth of the three transverse rows in which these plates are arranged, it seems likely that the inter-zonal exoskeleton has been formed in its ventral part by the fusion of the same number of rows of trunk-scales.

Not only in *Hemicyclaspis* but also in a great many other British forms the inter-zonal exoskeleton exhibits traces of the scales by the fusion of which it has been formed. Usually these traces are to be found only posteriorly, but in forms such as *Thyestes egertoni* (text-fig. 60; Pl. 52, fig. 3) they are, as in the Spitsbergen genus *Kiaeraspis* (Stensiö 1927, p. 24), also present somewhat further forwards. In this connection it may be pointed out that the dorsal portion of the inter-zonal exoskeleton always reaches further backwards on the trunk than the ventral portion, showing that the inter-zonal exoskeleton has incorporated more trunk-scales dorsally than ventrally. In *Kiaeraspis* it comprises scales belonging to at least one more row dorsally than ventrally (Stensiö 1927, p. 25), and in *Cephalaspis fletti* and *C. salweyi* scales belonging to at least three more rows, while in *Hemicyclaspis* its more ventro-medial part is not developed at all, but, as we have seen, is represented by independent plates only.

The total number of transverse rows of scales taking part in the formation of the inter-zonal exoskeleton could not be established with absolute certainty in any of the British species studied, but it is clear that it was proportional to the length of the inter-zonal part. As far as can be judged from our present knowledge of the British species, it is very likely that the number of rows so included is somewhat greater than I first supposed (Stensiö 1927, p. 25); thus there are probably at least 4 in *Hemicyclaspis murchisoni,* from 4 to 7 in the majority of the species of *Cephalaspis,* about 7 or 8 in *Thyestes egertoni,* 10 or 11 in *Kiaeraspis,* and upwards of 11 in *Didymaspis.* Since, as I have already pointed out in the monograph on the

Spitsbergen forms, there is evidence that the transverse rows of trunk-scales corresponded in number to the myomeres, it follows that the number of segments which took part in the formation of the inter-zonal part was probably equal to the number of transverse rows of scales which went to form its exoskeleton.

We may sum up the foregoing remarks by saying that the total number of transverse rows of scales forming the exoskeleton of the inter-zonal part may vary widely in different forms, and, moreover, the number of rows of scales included in the dorsal half always exceeds that in the corresponding ventral half, but the difference is not constant, varying with the species. Finally, it is also clear that the inter-zonal exoskeleton is not so definitely separated from the scales of the trunk as the account in my monograph on the Spitsbergen forms suggests; but in reality there is a more or less definite transitional area between the two, which is especially conspicuous in *Hemicyclaspis*, not only laterally on the flanks but also ventrally (text-figs. 8, 24; Pl. 6, figs. 1–3; Pl. 7, fig. 3).

With regard to the development of the posterior angle, the postero-lateral angles, the dorsal spine and the median dorsal longitudinal crest, the inter-zonal part in the British Cephalaspids is essentially similar to that of the Spitsbergen Cephalaspids (*cf.* Stensiö 1927, pp. 25–26).

Finally, the zonal or shoulder-girdle part of the abdominal division of the cephalic shield is found in a state of development similar to that of the Spitsbergen forms, except perhaps in *Ateleaspis*. In *Hemicyclaspis* (text-figs. 8, 15, 23–25, 27, 28; Pl. 2, fig. 1; Pl. 4, figs. 2, 4; Pl. 5, figs. 2, 5; Pl. 6, figs. 1, 2; Pl. 7, fig. 3; Pl. 8, fig. 4; Pl. 11, figs. 1, 2; Pl. 22, fig. 5) this part is, as in *Aceraspis* and *Micraspis*, without a cornu, and this may also have been the case in *Ateleaspis*, but the details are very imperfectly known. In *Didymaspis* (text-fig. 61A, B; Pl. 52, fig. 5; Pl. 54, fig. 1; Pl. 55, figs. 1, 4) it is uncertain whether the very conspicuous postero-lateral angle of the zonal part projected laterally towards the pectoral fin and thus formed a small cornu or whether it was as in *Hemicyclaspis*. In all the other British Cephalaspids each zonal part is provided with a pronounced cornu. Except perhaps in *Ateleaspis*, a pectoral sinus is present in all the British forms, although it may be variously developed. This sinus lacks lateral boundaries in *Hemicyclaspis*, in which, being destitute of cornua, it is not so conspicuous as in the other genera (text-figs. 8, 15, 23–25).

Pectoral fins covered with scales are preserved in several of the British forms, and these are seen to have articulated with the posterior surfaces of the zonal parts (*Pec*, text-figs. 15, 23, 25; Pl. 1, figs. 1, 2; Pl. 2, figs. 1, 4; Pl. 3, fig. 4; Pl. 4, fig. 2; Pl. 7, fig. 3; Pl. 8, fig. 3; Pl. 28, fig. 3; Pl. 30, figs. 1, 4; Pl. 31; Pl. 37, fig. 3; Pl. 40, fig. 1; Pl. 43, figs. 1, 2).

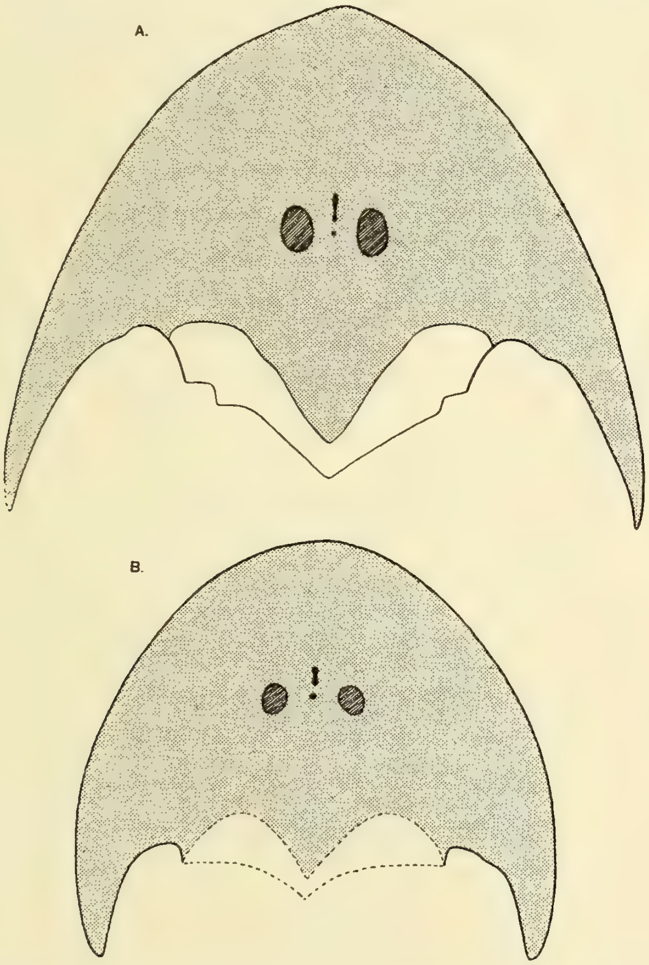
As noted above, the zonal part of *Ateleaspis* seems to differ somewhat from that in typical Cephalaspids. This, however, is perhaps more apparent than real, for all the *Ateleaspis* material found so far is so badly preserved that it is very difficult to determine with certainty either the outlines of the cephalic shield or the presence or absence of a pectoral fin. In 1927 I wrote concerning the inter-zonal part and the pectoral fin of *Ateleaspis* as follows (Stensiö 1927, pp. 26–28): " In *Ateleaspis* the postero-lateral ' lappet-like expansions ' of the cephalic shield were considered by Traquair (1899*b*, pp. 858; 1905, pp. 885–886) to be homologous with the ' flap-like ' structures in *Cephalaspis, i.e.* with the structures called in this work the pectoral fins. It seems not improbable, however, that the ' lappet-like expansions ' in *Ateleaspis*—if they really were as in the restoration given by Traquair—instead represent the cornua and perhaps certain proximal parts of the pectoral fins, and that both are in a much reduced state. Another possibility, which also is to be taken into account, is that the ' lappet-like expansions ' are only the cornua and that the pectoral fins were in a much reduced state and devoid of scales so that nothing therefore could be left of them in the fossils. In any case, from what has been said above concerning the presence of pectoral fins in Cephalaspids and other Ostracoderms it seems highly probable that the peculiar appearance of the postero-lateral parts of the cephalic shield in *Ateleaspis* are due to reductions and transformations of conditions rather like those in *Cephalaspis*. This is the more probable since *Ateleaspis* in most other respects obviously is a typical Cephalaspid." At present I am more inclined to believe that pectoral fins were present in *Ateleaspis* although devoid of scales; and if this was so, it follows that it would depend on the breadth of the proximal parts of these fins whether the postero-lateral angle of each zonal part projected laterally as a cornu or was as in *Hemicyclaspis*. In any case, I do not consider it probable that the zonal part and the pectoral fin in *Ateleaspis* were fundamentally different from those of *Hemicyclaspis*, *Aceraspis* and *Micraspis*.

Exoskeleton and endoskeleton of the cephalic shield.—The exoskeleton and the endoskeleton of the cephalic shield of the British Cephalaspids are in position, extent and mutual relations exactly as in the Spitsbergen Cephalaspids (*cf.* Stensiö 1927, pp. 28–32). The exoskeleton is, however, generally both better and more completely preserved, and on that account could be studied in greater detail; a description of it is given in the account of the microstructure of the bone-tissue of the cephalic shield (pp. 13–27). The endoskeleton, on the contrary, is usually much less perfectly preserved than in the Spitsbergen forms. Its extent backwards is well displayed in several of the species, such as *Cephalaspis whitei*, *C. powriei*, *Thyestes egertoni*, *T. salteri*, *Didymaspis* and others (text-figs. 3, 4, 61B), comprising, as in the Spitsbergen forms, the endocranium, the dorsal parts of the visceral endoskeleton and the endoskeletal shoulder-girdle. A pronephros component has not yet been observed, but it is very likely that such a component was present in its normal state of development.

In *Sclerodus* [*Eukeraspis*], *Didymaspis*, *Thyestes*, *Securiaspis* and perhaps also in *Benneviaspis* the endoskeleton was cartilaginous internally and as a rule provided with perichondrial bone-layers to about the same extent as in *Kiaeraspis* and *Cephalaspis hoeli* from the Downtonian of Spitsbergen (*cf.* Stensiö 1927, pp. 30–31). Thus in *Sclerodus* [*Eukeraspis*], *Didymaspis* and *Thyestes*, in which the details are best known, we find that it was covered by an internal bone-layer, a labyrinth bone-layer, an orbital bone-layer, an external bone-layer and canal bone-layers, all of which seem to be complete and continuous with each other and with the exoskeleton.

In the other British genera, *e.g. Hemicyclaspis* and *Cephalaspis*, the endoskeleton of the cephalic shield was also cartilaginous internally, but in these the perichondrial bone-layers were neither so strongly nor so completely developed and may have been almost entirely absent.

We will now turn to *Hemicyclaspis murchisoni* and to several of the species of *Cephalaspis* for particulars concerning the degree of development of the perichondrial bone-layers.

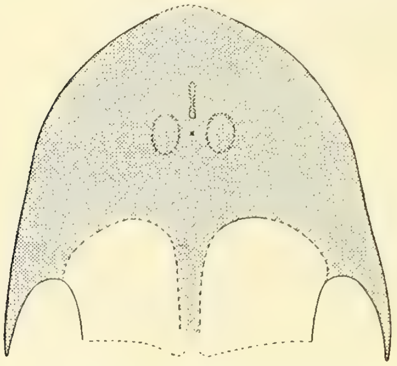


TEXT-FIG. 3.—Sketches showing the extent of the endoskeleton of the cephalic shield. Endoskeleton denoted by shading. A, in *Cephalaspis whitei*, sp. nov.; B, in *C. powriei* var. ? *asper* LANKESTER.

In *Hemicyclaspis murchisoni* the internal layer has not been identified with certainty, probably because it was usually too delicate to be preserved, or else entirely absent. However, the labyrinth, orbital, external and canal layers immediately below the exoskeleton are to be seen in certain specimens, but they are generally delicate and in an imperfect state of preservation, especially the labyrinth and external layers, which on that account are preserved only in exceptional cases (Pl. 5, fig. 5; Pl. 8, fig. 4; Pl. 22, fig. 5).

In *Cephalaspis salweyi* the perichondrial bone-layers are usually very imperfectly preserved, so that little can be found out about them. In one specimen (B.M., P. 189), however, a representative portion of each layer, although so very fragile, has been exposed by preparation (Pl. 25, fig. 1). In this specimen they are as follows: the internal layer is present from the naso-hypophysial opening in front at least as far back as the middle of the otic region; the labyrinth layer, which is more delicate than most of the others, seems to have lined at least the main part of the labyrinth cavity; the orbital layer is in part fairly well developed, and so also is the external layer where it lined the anterior half of the oralo-branchial chamber, but in the posterior half no certain traces of it could be discovered, so that it was either absent or perhaps present only in places. Finally, most of the canal layers are present, but a great many of them seem to be more delicate in *C. salweyi* than in the majority of the Cephalaspids.

In *C. whitei* no remains could be discovered of the labyrinth layer, and as the available material of this species is fairly extensive it is probable that this layer was entirely absent. The internal layer seems also to be generally absent, but in one case I believe that I could detect faint traces of it. The orbital layer is incompletely known, but it is not unlikely that it was fairly well developed. The external layer appears to have been present to about the same extent as, or even more completely than, in *C. salweyi*. The canal layers are well developed immediately below the exoskeleton, but somewhat deeper in the endoskeleton they are, as a rule, entirely absent.



TEXT-FIG. 4.—*Thyestes salteri* (EGERTON). Sketch showing the extent of the endoskeleton of the cephalic shield.

In *C. pagei*, *C. powriei*, *C. agassizi*, *C. lyelli*, *C. heightingtonensis*, *C. lornensis*, *C. lankesteri*, *C. fletti*, *C. langi*, *C. watsoni* and certain indeterminable species of *Cephalaspis* the perichondrial bone-layers seem to have been developed very much as in *C. salweyi* or *C. whitei*.

Finally, in the other species very little is known of the perichondrial bone-layers, except the canal layers, of which the most superficial are often well developed. It is therefore likely that in these species the internal layer, the labyrinth layer and the external layer were all either completely absent, or at least too delicate to be preserved in the fossils.

From the above facts it is obvious that the British species of *Cephalaspis* had as a rule but a moderately ossified endoskeleton. As these species constitute the majority of the British Cephalaspids and as they are all from lower Devonian deposits, we find that the British Cephalaspids show similar regressive conditions in regard to the degree of ossification of the endoskeleton as the Spitsbergen Cephalaspids from deposits of corresponding age. Accordingly, we have here additional support for the opinion advanced by the present writer in 1927 (STENSIÖ 1927, pp. 31–32) that the Cephalaspids in general during the time from the Upper Silurian to the

Lower Devonian underwent regressive development with regard to the degree of ossification of the endoskeleton.

Micro-structure of the bone-tissue of the cephalic shield.[1]—The exoskeleton of the cephalic shield of the British Cephalaspids is as a rule well developed and strong, not only in the Downtonian, but also in the Devonian forms. As in the Spitsbergen species, it is thickest and strongest in the circum-orbital ridge, along the lateral borders of the dorsal electric field, in the dorsal median crest and spine, along the rostral and lateral margins of the shield, and in those parts which are situated on the cornua (Pl. 32, fig. 6). In the British forms also we may distinguish in it three different layers: a superficial layer, a middle layer, and a basal layer (for a more detailed description and definition of these layers, etc., see Stensiö 1927, pp. 34–40).

The superficial layer is always rather badly preserved, but despite this it is clear that it consists of dentine which near the surface approaches enamel in character (*sl*, Pl. 57, fig. 2; Pl. 60, figs. 2–4; Pl. 63, figs. 2, 3). As a rule its dentine-canals seem to reach the external surface, there opening by extremely fine perforations. In many of the forms it is, in addition, perforated by fairly wide pores of a special canal system, the mucous canal system. These pores, which pierce it from below and ascend to its outer surface, are considerably wider than the openings of the dentine-canals, and they are therefore clearly visible to the naked eye or under low power (p, p_1, text-figs. 6, 7; Pl. 9; Pl. 56, fig. 2; Pl. 57, figs. 2, 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3), whereas the openings of the dentine-canals are discernible only under a very high power. When in the following account pores are mentioned as piercing the superficial layer, it is always these pores of the mucous canal system that are meant.

As in the Spitsbergen Cephalaspids, the superficial layer is very varyingly distributed in the different species. In *Hemicyclaspis murchisoni* (*sl*, text-fig. 7; Pl. 1, figs. 1–3; Pl. 4, fig. 4; Pl. 5, fig. 6; Pl. 8, fig. 3; Pl. 9; Pl. 57, figs. 2, 3; Pl. 60, figs. 1–4; Pl. 64, fig. 1; Pl. 65, fig. 1), *Cephalaspis whitei, C. whitbachensis, C. fletti, C. lornensis, C. lankesteri, Benneviaspis lankesteri,* and several others (*sl*, Pl. 17, fig. 3; Pl. 47, fig. 1; Pl. 56, fig. 2; Pl. 59, fig. 3; Pl. 64, figs. 2, 3) it generally forms a continuous covering to the middle layer throughout the cephalic shield. In these species, therefore, it is not subdivided into polygonal areas by any inter-areal grooves since, as we shall see later, open grooves of this kind are here absent except in rare cases, and then only in the inter-zonal part at its more posterior end, where they are represented only by faint traces (Pl. 9). When tubercles are present on the exoskeleton of these species they are, at least very largely, thickenings of the superficial layer.

In a second group of species, to which *Cephalaspis agassizi* (Pl. 22, fig. 4), *C. salweyi* (Pl. 11, fig. 4; Pl. 12, fig. 3; Pl. 13, fig. 1; Pl. 32, fig. 1; *sl*, Pl. 58, fig.

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[1] For the micro-structure of the ventral visceral exoskeleton see the description on pp. 43–44. The exoskeletal plates covering the electric fields are to a certain extent dealt with here. Additional notes on them are to be found in the description of the electric fields below (p. 47). For the micro-structure of the scales see the account of the division of the trunk following the cephalic shield (pp. 60–62).

3; Pl. 66, fig. 1), *C. watsoni* (Pl. 19, figs. 3, 4), *C. woodwardi* (Pl. 20, figs. 1, 2), *Hemicyclaspis* (?) *lightbodii* (Pl. 10, fig. 3; Pl. 11, fig. 2; Pl. 63, figs. 2, 3) and certain other species belong, the superficial layer is present chiefly or only in the tubercles forming the ornamentation of the exoskeleton, and thus the spaces between the tubercles are to a considerable extent, or even wholly, uncovered by the superficial layer, so that the middle layer is more or less completely exposed in the fossil condition.

In a third group, which includes *C. powriei* and *C. pagei* (*sl*, Pl. 29, figs. 1, 3; Pl. 31; Pl. 32, fig. 4; Pl. 36, fig. 4; Pl. 39, fig. 1; Pl. 42, figs. 1, 2; Pl. 43, figs. 1, 2; Pl. 44, fig. 1) and perhaps also certain other species, we find that the superficial layer is subject to considerable variation even among individuals of the same species; thus in some individuals it may be complete and continuous throughout the cephalic shield, whereas in others it may occur in patches or be entirely subdivided into isolated tubercles.

Finally, in a fourth group of species, represented by *Sclerodus* [*Eukeraspis*] *pustuliferus*, *Didymaspis grindrodi* (Pl. 45, fig. 1; Pl. 52, fig. 1; Pl. 53, figs. 1–4; Pl. 54, figs. 1–3; Pl. 55, figs. 3, 4) and the species of *Thyestes* (Pl. 27, figs. 3, 4), the superficial layer seems to be either entirely absent or else to form only a small distal part of the tubercles which constitute the ornamentation of the exoskeleton. In any case, it is clear that it is very slightly developed.

A species in which the superficial layer was developed as a continuous covering of the middle layer, but at the same time completely subdivided into polygonal areas by means of broad and deep inter-areal grooves throughout the cephalic shield, could not be found with certainty among the British Cephalaspids, whereas among the Spitsbergen Cephalaspids such species seem to have been fairly common (Stensiö, 1927).

The middle layer (*ml*, text-figs. 6, 7; Pl. 41, figs. 1, 2; Pl. 42, fig. 1; Pl. 44, figs. 1, 2; Pl. 45, figs. 2, 3; Pl. 56, fig. 2; Pl. 57, fig. 2; Pl. 58, fig. 2; Pl. 59, fig. 3; Pl. 60, figs. 1–4; Pl. 63, figs. 2, 3; Pl. 64; Pl. 66, fig. 1), like that in the Spitsbergen forms, passes gradually outwards into the superficial layer and inwards into the basal layer; thus it is as a rule without cell-spaces and distinct lamination in its superficial part, these characters gradually appearing near the basal layer. As in the Spitsbergen forms, this middle layer is especially characterized by its abundant vascular canals, which cause it to appear in transverse section as a mass of more or less thin trabeculae separated by numerous vacuities. As previously described, the principal and most conspicuous canals in it are the radiating vascular canals (*rad.c*) and their external branches (*ebc*). In addition to these, in several forms it lodges also a special canal system in those parts immediately beneath the superficial layer, a system which will be referred to as the *mucous canal system* (*iac*, *ita*, *mc*, text-figs. 5–7; Pl. 4, fig. 3; Pl. 9; Pl. 10, figs. 1, 2; Pl. 23, fig. 1; Pl. 24, fig. 2; Pl. 29, fig. 1; Pl. 32, fig. 4; Pl. 42, fig. 1; Pl. 56, figs. 2, 3; Pl. 57, figs. 2, 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3; Pl. 65, fig. 1).

Whereas the basal parts of the middle layer, except in a few forms, are always present and continuous throughout the exoskeleton of the cephalic shield, the superficial parts of that layer are very differently developed in different forms: they may be either completely developed and continuous like the basal ones; or present only in the tubercles which form the ornamentation of the exoskeleton; or else almost or entirely absent both in and between the tubercles. The degree of development of the superficial parts of the middle layer is in fact dependent on the degree of development of the superficial layer, so that these parts are complete and continuous when the superficial layer is well developed and continuous, but subdivided into isolated tubercles or absent when the superficial layer occurs only in isolated tubercles, or is almost or entirely absent. If we examine the various forms in detail we find the following:—

The middle layer is completely developed and has its superficial parts continuous in *Hemicyclaspis murchisoni* (text-fig. 7; Pl. 5, fig. 6; Pl. 8, fig. 3; Pl. 9; Pl. 10, fig. 1; Pl. 60, figs. 1–4; Pl. 64, fig. 1), several species of *Cephalaspis*, such as *C. whitei*, *C. lankesteri* (Pl. 17, fig. 3; Pl. 56, fig. 2), *C. whitbachensis*, *C. fletti*, *C. lornensis*, and in *Benneviaspis lankesteri* (Pl. 24, figs. 1, 2; Pl. 45, fig. 3; Pl. 56, fig. 3; Pl. 59, fig. 3; Pl. 64, figs. 2, 3), species in which, as we have seen, the superficial layer is continuous. It is also completely developed in those specimens of *Cephalaspis pagei* (Pl. 36, fig. 4; Pl. 43, fig. 1; Pl. 44, fig. 1) and *C. powriei* (Pl. 29, fig. 1; Pl. 32, fig. 4) which have a continuous superficial layer.

The superficial parts of the middle layer are imperfectly developed in *Hemicyclaspis*(?) *lightbodii* (Pl. 10, fig. 3; Pl. 63, figs. 2, 3), *Cephalaspis salweyi* (Pl. 32, fig. 1; Pl. 58, fig. 3; Pl. 66, fig. 1), *C. agassizi* (Pl. 22, fig. 4), *C. watsoni* (Pl. 19, fig. 4) and other species in which, as previously pointed out, the superficial layer is present only in isolated tubercles, and in those specimens of *C. pagei* and *C. powriei* in which the superficial layer is similarly developed (Pl. 31; Pl. 39, fig. 1; Pl. 40, fig. 1; Pl. 42, figs. 1, 2). In all these the middle layer is represented in the spaces between the tubercles mainly, or only, by its basal parts with the radiating canals, which are, as a result, conspicuous in these interspaces. In the tubercles (Pl. 63, figs. 2, 3; Pl. 66, fig. 1) we usually find the superficial parts of the layer more or less well developed, but always without mucous canals, since these occur only between the tubercles.

The middle layer of *Thyestes* and *Didymaspis*, in which the superficial layer is almost or entirely absent, is imperfectly developed, both in its superficial and basal parts. In *Thyestes* it seems to be in the main as in *C. salweyi* and similar species, except that in its basal parts it is thinner and in the anterior rostral region of the cephalic shield even partly absent. In *Didymaspis* it is still more imperfect (Pl. 45, fig. 1); for in this genus it occurs over the greater part of the rostral region only in isolated tubercles, between which the basal layer is exposed in the fossil condition, and it is only towards the posterior margin of the inter-zonal part that its basal portion with the radiating canals is first clearly developed as a continuous covering of the basal layer.

In *Sclerodus* [*Eukeraspis*] the middle layer is thick and well developed, but differs from that in all other forms described in that it contains no distinct radiating canals, and all its vascular canals have an irregularly winding course, anastomozing frequently with each other, and therefore not arranged so as to correspond to any polygonal areas, which, in fact, are not to be observed in this genus. On account of the scarcity of material of *Sclerodus* suitable for making microscopic sections, no detailed study could be made of its middle layer.

The basal layer (*bl*, text-fig. 6; Pl. 5, fig. 6; Pl. 8, fig. 3; Pl. 9; Pl. 10, fig. 1; Pl. 24, fig. 2; Pl. 41, figs. 1, 2; Pl. 44, figs. 1–3; Pl. 45, figs. 1, 3; Pl. 58, figs. 2, 3; Pl. 59, figs. 3–5; Pl. 60, fig. 1; Pl. 63, figs. 1–3; Pl. 64, figs. 1–3; Pl. 65, fig. 1; Pl. 66, figs. 1–4) is always well developed and is in all forms continuous throughout the cephalic shield. As in the Spitsbergen species, it consists of laminated bone with numerous cell-spaces, and the canals of the sub-aponeurotic (sub-cutaneous) vascular plexus lie partly beneath and partly within its most basal part. Normally, it is perforated by the ascending vascular canals (*c.asc*) and, as we shall see from the account given below, also by certain other vascular canals.

In those British forms in which the micro-structure of the exoskeleton was studied, indications of resorption phenomena could be seen in two cases only, one a specimen of *Cephalaspis salweyi* (Pl. 63, fig. 1; Pl. 66, figs. 3, 4), and the other a specimen of *Hemicyclaspis murchisoni* (Pl. 65, fig. 1); and in both these it was the basal layer only that was affected.

In *Ateleaspis* the structure of the exoskeleton is not known in detail, but, so far as can be understood from TRAQUAIR'S description of it, it was essentially of the normal Cephalaspidean type. (TRAQUAIR 1899*b*, pp. 834–835; Pl. 4, figs. 9, 10: 1904, p. 885; Pl. 2, figs. 9, 10; Pl. 3, figs. 1, 2.)

In the monograph on the Spitsbergen Cephalaspids I showed that in several of these the external parts of the exoskeleton were subdivided into polygonal areas by means of well-defined open grooves connected with one other to form a network with wide meshes. These grooves, which may reach as far down as the transition between the superficial and basal parts of the middle layer, I termed *inter-areal grooves*, and I concluded that they were conceivably the equivalents of the so-called mucous canals of *Tremataspis* (STENSIÖ, 1927, pp. 33–40). More accurate details of the relations of these inter-areal grooves with the vascular canals could not be gained from the Spitsbergen material.

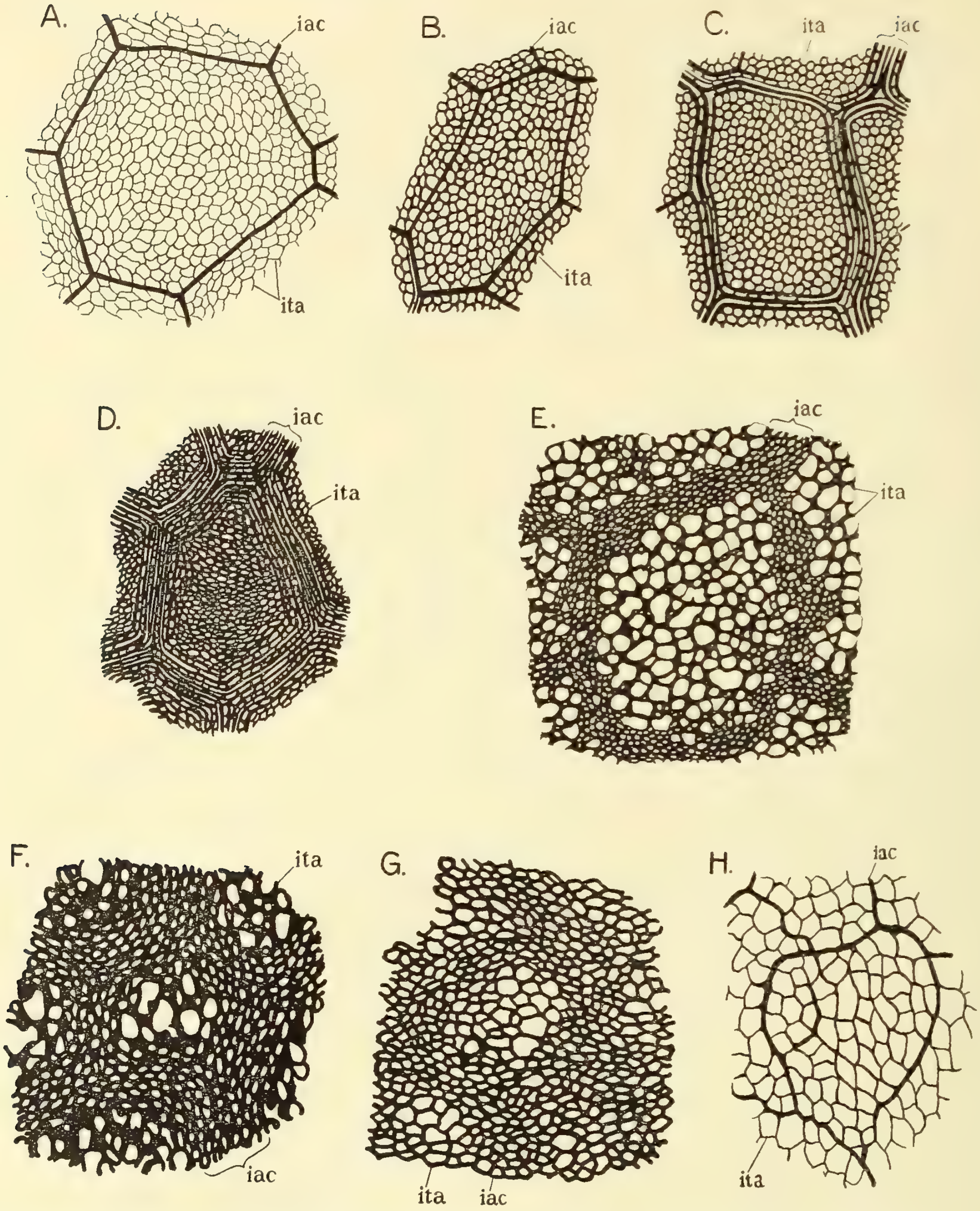
In certain of the Spitsbergen Cephalaspids, such as *Cephalaspis hoeli*, *C. vogti*, *Benneviaspis holtedahli*, *Hoelaspis angulata* and *Kiaeraspis auchenaspidoides*, I pointed out that I was unable to find any traces of inter-areal grooves. In all these forms the superficial layer was found to be well developed, forming a continuous covering to the middle layer throughout the cephalic shield and to be perforated by numerous, fairly wide pores opening on to the external surface of the layer. Among the British Cephalaspids we also find a great many species which show these features (p, p_1, text-figs. 6, 7; Pl. 9; Pl. 17, fig. 3; Pl. 36, fig. 4; Pl. 43, fig. 1; Pl. 44, fig. 1; Pl. 56, fig. 2; Pl. 57, figs. 2, 3; Pl. 59, fig. 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1, 3). Such species are, among others, *Hemicyclaspis murchisoni*, *Cephalaspis whitei*, *C. lankesteri*, *C. whitbachensis*, *C. fletti*, *C. lornensis*, certain indeterminable species of *Cephalaspis*, *Benneviaspis lankesteri* and in several cases also

C. pagei and *C. powriei.* However, in some of these species, such as *H. murchisoni* and a few of *Cephalaspis,* we notice on closer examination that there are, at least in certain specimens or in certain places, fairly wide canals in the external parts of the middle layer (*iac,* text-figs. 5A, B, H, 6; Pl. 4, fig. 3; Pl. 10, fig. 2; Pl. 23, fig. 1; Pl. 24, figs. 1, 2; Pl. 45, fig. 3; Pl. 56, fig. 3; Pl. 59, fig. 3; Pl. 64, figs. 2, 3). These canals anastomose with each other, forming a wide-meshed network which subdivides the superficial parts of the middle layer into polygonal areas. Since these polygonal areas agree with those that are bounded by the inter-areal grooves in the Spitsbergen forms not only in size and position in the exoskeleton, but also in the arrangement of the vascular canals within and below them, it is obvious that they are homologous with them; and it follows, of course, that the canals by which they are bounded must be the homologues of the inter-areal grooves of the Spitsbergen forms. These canals, therefore, will be referred to in the following account as *inter-areal canals.*

In addition to the inter-areal canals, we find in the exoskeleton of those British Cephalaspids in which the superficial layer forms a continuous covering to the middle layer, a great number of other canals, generally of fine dimensions, situated in the most superficial part of the middle layer, in the meshes formed by the inter-areal canals, and superficially to both the radiating canals and their wider external branches. These fine canals thus lie in the polygonal areas themselves, and they will therefore be called the *intra-areal canals.*

These intra-areal canals (*ita,* text-figs. 5–7; Pl. 4, fig. 3; Pl. 9; Pl. 10, fig. 2; Pl. 24; Pl. 45, fig. 3; Pl. 56, fig. 3; Pl. 64, figs. 2, 3) lie immediately beneath the superficial layer and anastomoze frequently with each other and with the inter-areal canals, thus forming a network of fine mesh within the wide meshes of the inter-areal canals. Both from their position and relations it is obvious that they are of the same nature as the inter-areal canals; and it is not difficult to see that the two together are homologous with the mucous canal system of *Tremataspis,* the inter-areal canals corresponding exactly to the wide primary, and the intra-areal canals to the narrower secondary, mucous canals of *Tremataspis* (*cf.* Patten 1912, pp. 290–292, figs. 193–195; and Stensiö 1927, pp. 38–39; Pl. 72, figs. 1, 2): on this account they will in the present work be referred to together as the *mucous canal system.* From this it follows, of course, that the inter-areal grooves described in certain of the Spitsbergen forms must also belong to the mucous canal system (*cf.* Stensiö 1927, p. 39) and be imperfectly enclosed inter-areal mucous canals. It may be mentioned here that both the inter-areal and intra-areal canals in the British Cephalaspids open outwards by means of the numerous, fairly wide pores which, as already pointed out, ascend through the superficial layer to its external surface (*p,* text-figs. 6, 7; Pl. 9; Pl. 36, fig. 4; Pl. 42, fig. 1; Pl. 44, fig. 1; Pl. 56, fig. 2; Pl. 57, fig. 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3).

From what has now been said of the British forms it follows that a mucous canal system, consisting of closed canals in the exoskeleton, is present in all Cephalaspids in which a continuous superficial layer perforated by numerous pores is found. Accordingly, the reason why I was unable to find any inter-areal grooves in *Cephal-*



Text-fig. 5.—Sketches showing the arrangement of the mucous canals in certain forms.

A, from a specimen of *Hemicyclaspis murchisoni* in which the inter-areal canals are wide and not subdivided; B and C, from a *Cephalaspis* of indeterminable species, in which the inter-areal canals around certain of the polygonal areas are undivided (B), whereas around other polygonal areas they are subdivided into two or more canals (C); D, from *Cephalaspis campbelltonensis*, in which the inter-areal canals are subdivided into numerous canals around all the polygonal areas; E, from *Cephalaspis powriei* var. *brevicornis* in which the inter-areal canals are much modified, forming a fine network; F, from *Cephalaspis powriei* (holotype) in which the inter-areal canals also are much modified, forming a network; G, from *Hemicyclaspis murchisoni* var. *ludlowensis* in which the conditions on the whole are much as in the holotype of *C. powriei*; H, from a specimen of *Cephalaspis* sp. in which the inter-areal canals are undivided and the plexus of the intra-areal canals is of fairly wide mesh. Approximate magnifications: A, B and C, × 20 diam.; D, × 6 diam.; E, × 9 diam.; F, × 20 diam.; G, × 12 diam.; and H, × 10 diam.

iac, inter-areal canals; *ita*, intra-areal canals (in some figures not clearly distinguishable from the inter-areal canals).

aspis hoeli, C. vogti, Benneviaspis holtedahli, Hoelaspis angulata and *Kiaeraspis auchenaspidoides* was simply that these grooves, as well as the intra-areal canals, are in those species completely closed and situated in the exoskeleton. It should be mentioned, however, that in the forms in which the superficial layer is continuous only in each polygonal area and there perforated by numerous pores (*e.g.* in those specimens in which the superficial layer is continuous but subdivided into polygonal areas by imperfectly closed inter-areal canals), the intra-areal canals only are enclosed in the exoskeleton.

From these facts it is also clear that all the pores which open on to the external surface of the superficial layer, and which are discernible either with the naked eye or with a very low magnification, belong to the mucous canal system: thus they do not issue from the sub-epidermal vascular plexus, as maintained by the present writer in 1927 (Stensiö 1927, p. 36). To that faulty conclusion I was led by the bad state of preservation of the exoskeleton of the Spitsbergen forms, which rendered it impossible for me to observe the intra-areal canals sufficiently clearly to see that they could not belong to the sub-epidermal vascular plexus.

Finally, in those British Cephalaspids in which the superficial parts of the exoskeleton (the superficial layer and the external parts of the middle layer) are not continuous but present in isolated tubercles only, we find no closed mucous canals, but often more or less distinctly developed grooves between the tubercles, and these, as shown by their course, position and relations, unquestionably represent the mucous canal system. Generally these grooves correspond to the inter-areal mucous canals only (*iac*, Pl. 9; Pl. 10, fig. 3; Pl. 32, fig. 1; Pl. 40, fig. 1), but in certain instances it is clear that in addition there are grooves representing the intra-areal mucous canals (*ita*, Pl. 10, fig. 3; Pl. 42, figs. 1, 2). In several of these British forms, however, there are neither grooves nor other indications of the mucous canal system, either in or on the exoskeleton; and this is especially the case in those forms in which the superficial parts of the exoskeleton are much reduced. That the mucous canal system was, nevertheless, usually present in these forms is clearly shown by the arrangement of the vascular canals of the exoskeleton; and the reason for the absence of grooves or markings on the exoskeleton is here simply due to the fact that the mucous canal system was entirely surrounded by soft tissue, or, expressed in another way, to the fact that it lay entirely superficially to the exoskeleton. Ultimately this state of the mucous canal system depends on the extent to which the superficial parts of the exoskeleton have been suppressed and not to a shifting outwards of the mucous canal system.

In the Spitsbergen forms in which the superficial parts of the exoskeleton are imperfectly developed, the mucous canal system gave rise to grooves only on the exoskeleton, or lay more or less completely superficially to it, just as in the corresponding British forms.

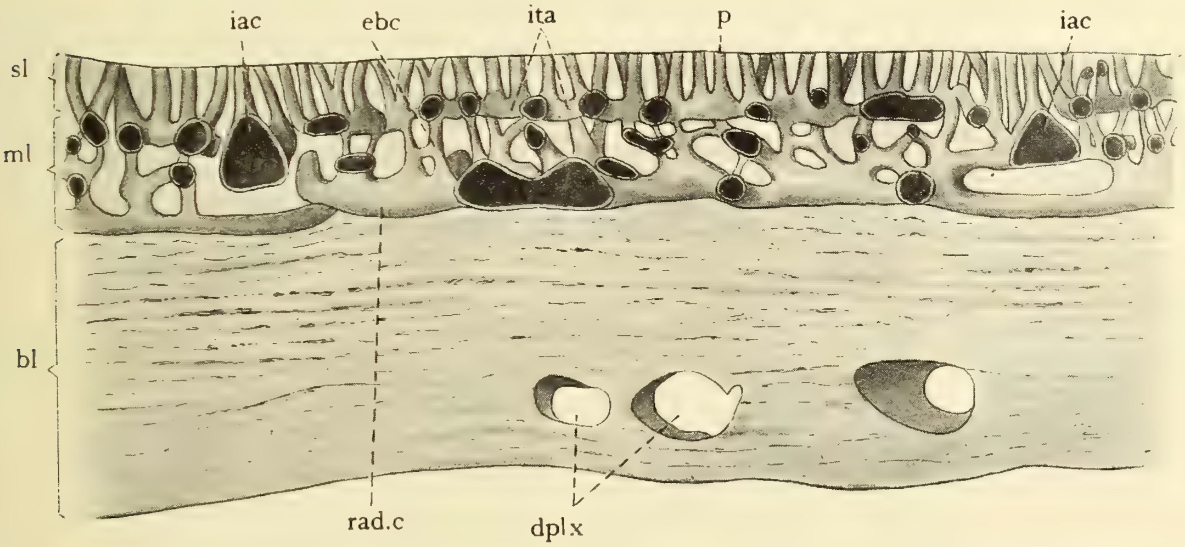
From the foregoing account we see that a mucous canal system was present in all Cephalaspids and that this canal system is completely enclosed in the exoskeleton in those cases where the superficial parts were continuous and completely developed, but was very largely, or even entirely, outside the exoskeleton when the superficial parts were less perfectly developed. Accordingly, we find that the relations between the mucous canal system and the exoskeleton were dependent on the degree of development of the exoskeleton, or to be more exact, on the degree of development of the superficial parts of the exoskeleton.

We will now proceed to a more detailed account of the mucous canal system in the different British forms.

In many of the British species of *Cephalaspis* and in *Hemicyclaspis* (?) *lightbodii* the mucous canal system exhibits on the whole the simple conditions described above. Thus the inter-areal canal or inter-areal groove between two neighbouring polygonal areas is always single, and not subdivided into two or more, and is, in addition, wider (*iac*, Pl. 10, figs. 2, 3; Pl. 23, fig. 1; Pl. 24, figs. 1, 2; Pl. 32, fig. 1; Pl. 56, fig. 3; Pl. 64, figs. 2, 3) than the intra-areal canals or grooves which form a fine-meshed network—the intra-areal mucous plexus—with each other (*ita*, Pl. 10, figs. 2, 3; Pl. 24, figs. 1, 2; Pl. 56, fig. 3; Pl. 64, figs. 2, 3). There is, therefore, in this group a marked difference between the inter- and intra-areal mucous canals. Many of the forms in which the superficial layer is represented merely by isolated tubercles belong to this group, and, since often in these forms the intra-areal canals gave rise to no markings in the exoskeleton, we find here several with inter-areal grooves only.

In another group of species of *Cephalaspis* the mucous canal system is characterized by the inter-areal canal between two adjacent polygonal areas being subdivided into two or more concentric canals (*iac*, text-fig. 5C; Pl. 45, fig. 3), which are fairly narrow and anastomoze with each other by means of short branches. In some species of this group, however, there are in places polygonal areas surrounded only by a single undivided inter-areal canal (*iac*, text-fig. 5B; Pl. 45, fig. 3). The intra-areal canals (*ita*, text-fig. 5B, C; Pl. 45, fig. 3) in this group are always fine and form a plexus similar to that in the group first described, and are thus easily distinguishable from the inter-areal canals. Among the Canadian Cephalaspids, *Cephalaspis campbelltonensis* (text-fig. 5D; Pl. 45, fig. 2) has the inter-areal canals throughout the cephalic shield subdivided into four, five or more fine canals which anastomoze frequently with each other to form a fine-meshed plexus. Thus the inter-areal canals here tend to develop in a way similar to the intra-areal canals. *C. campbelltonensis* is, however, a typical representative of the group under consideration, which, as far as is known, comprises only species of Cephalaspids with a continuous superficial layer.

In a third group of species represented, among others, by *Cephalaspis pagei* and *C. powriei* (*iac, ita, mc*, text-fig. 5E, F; Pl. 29, fig. 1; Pl. 31; Pl. 32, fig. 4; Pl. 36, fig. 4; Pl. 40, fig. 1; Pl. 42; Pl. 43, fig. 1; Pl. 44, fig. 1), the inter-areal canals are often in places, or throughout their extent, subdivided into numerous fine canals which anastomoze frequently with each other and which are developed in such a way that they much resemble the intra-areal canals: in fact in such cases much of, or even the entire, mucous canal system tends to form a uniformly fine-meshed plexus throughout the cephalic shield, a plexus in which it is often difficult to distinguish the inter-areal from the intra-areal canals. In *C. powriei* and its varieties the arrangement of the mucous canal system seems to be more constantly developed in the way just described than is the case in *C. pagei*, and moreover the inter-areal canals, even when they are much subdivided, are still distinguishable from the intra-areal canals; for they usually retain a certain concentric arrangement and, in addition, their meshes are much smaller than those formed by the intra-areal canals. In *C. pagei*, on the contrary, the state of the inter-areal canals is most variable; for, while in many examples they are single throughout, in others they are much subdivided and so developed that it is impossible to distinguish them from the intra-areal canals, the whole mucous canal system being developed as a uniform, very fine-meshed network. As has already been pointed out, in those specimens of *C. pagei* and *C. powriei* in which the superficial parts of the exoskeleton are complete and continuous, the entire mucous canal system is developed as a system of closed canals within the exoskeleton; whereas in those specimens in which these parts are present merely in isolated tubercles, it is represented only by shallow and indistinct, open grooves on the exoskeleton. It should be mentioned that in *C. pagei* the mucous canal system in certain specimens may be in the form of closed canals in the central parts of each polygonal area (*a*, Pl. 42, fig. 1) but of open grooves towards the periphery (*b*, Pl. 42, fig. 1). In such specimens the central parts of the polygonal areas are, of course, provided with a continuous superficial layer, and it is thus obvious that these specimens approach in this respect those Spitsbergen forms in which the superficial layer is continuous but subdivided into polygonal areas by



TEXT-FIG. 6.—Sketch showing a transverse section through the exoskeleton of a species of *Cephalaspis* in which the superficial layer forms a continuous covering to the middle layer. The sketch is intended to give an idea of the position of the mucous canals, their mode of opening outwards and their relations to the underlying vascular plexus. × 200 diam.

bl, basal layer; *dplx*, canals belonging to the sub-aponeurotic (sub-cutaneous) vascular plexus; *ebc*, external branches of the radiating canals; *iac*, inter-areal canals; *ita*, intra-areal canals; *ml*, middle layer; *p*, pores by means of which the mucous canals open outwards; *rad.c*, radiating canals; *sl*, superficial layer.

means of the inter-areal grooves, which, as we have already noted, represent the inter-areal canals.

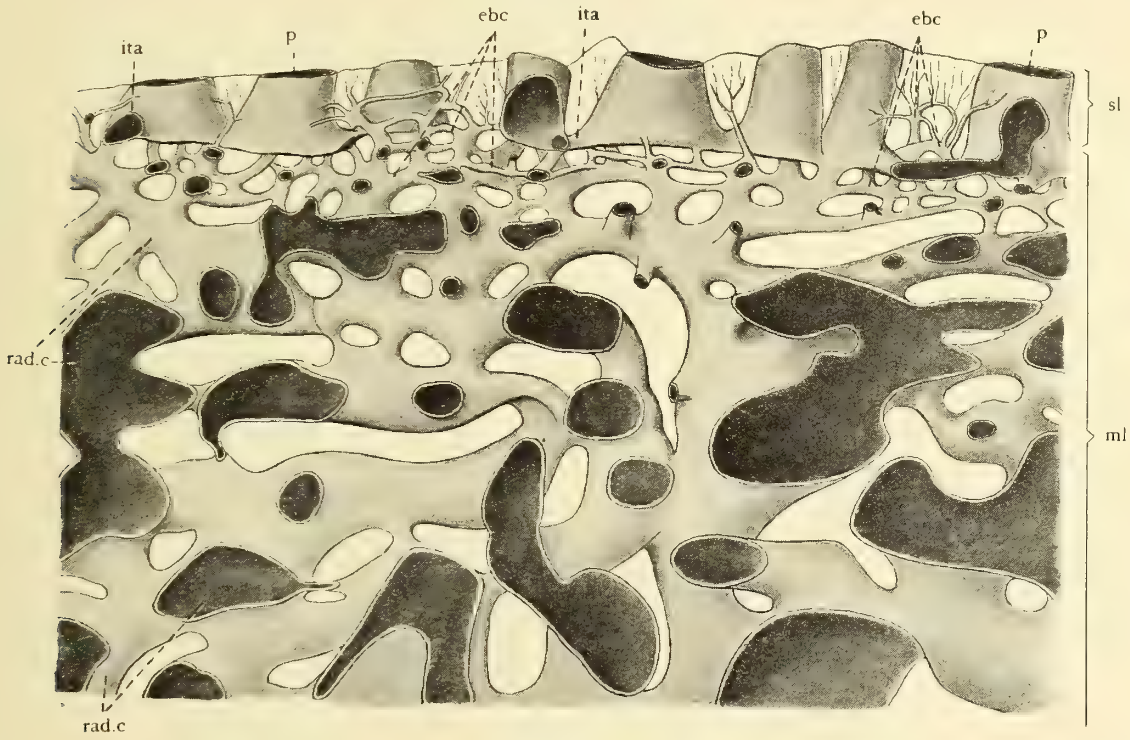
Hemicyclaspis murchisoni seems to resemble most in its mucous canal system *C. pagei*, and it may therefore be referred to the same group as *C. pagei* and *C. powriei*. In certain specimens of *H. murchisoni* there is, at least in a considerable part of the posterior end of the cephalic shield, only a single, wide canal between the neighbouring polygonal areas, whereas the intra-areal canals form a fine-meshed plexus in the normal way (text-fig. 5A; Pl. 4, fig. 3; Pl. 10, fig. 2). In these specimens, therefore, the mucous canals are developed, at least in places, in a very simple way, with the inter- and intra-areal canals clearly distinguishable from one other. In most specimens, however, the inter-areal canals are transformed into a fine-meshed plexus which differs only slightly from the intra-areal plexus (text-fig. 5G; Pl. 9; Pl. 57, fig. 3), so that these two series of canals are difficult to distinguish from one another, and the mucous canal system as a whole constitutes a fairly uniform, fine-meshed plexus. In contrast to that in *C. powriei* and *C. pagei*, the mucous canal system of *H. murchisoni* always consists of closed canals in the exoskeleton. We thus find that this canal system in the development of its inter-areal canals may be subjected to very considerable variations, not only in different individuals of the same species, but also in different places on the cephalic shield of the same specimen. It is therefore obvious that it is of limited importance from a taxonomic point of view.

In a fourth group comprising *Cephalaspis lankesteri*, *C. whitei*, *C. fletti*, *C. whitbachensis*, *C. langi* and probably several others, the mucous canal system seems to be developed usually as a uniformly fine-meshed plexus in which it is impossible to distinguish between inter- and intra-areal canals (Pl. 56, fig. 2). In this group the superficial parts of the exoskeleton are always completely developed and continuous throughout the cephalic shield.

In *Thyestes egertoni*, *Thyestes salteri* and *Didymaspis grindrodi* there are, as in *Thyestes verrucosus* (*cf.* Stensiö 1927, pp. 37–38), no grooves or other distinct markings of the mucous canal system, either in or on the exoskeleton of the cephalic shield (text-fig. 60; Pl. 27, figs. 3, 4; Pl. 45, fig. 1; Pl. 54, fig. 3; Pl. 55, fig. 3). As, however, the vascular canal system of the exoskeleton in the posterior part of the cephalic shield in these species is arranged in a way similar to that in the forms with mucous canals or grooves, I am of the opinion that a mucous canal system was really present in them also, although, as has already been pointed out, this system must have been completely external to the exoskeleton, doubtless owing to the almost complete absence of both the superficial and middle layers (pp. 14, 15).

Finally, *Sclerodus* [*Eukeraspis*] *pustuliferus* shows, like the species of *Thyestes* and *Didymaspis grindrodi*, no markings whatever of any mucous canals. As, moreover, it has no radiating canals, nor have its vascular canals any arrangement resembling that present in forms in which a mucous canal system occurs, it seems very possible that it was entirely devoid of such a canal system.

From the account given above it is fully evident that, as supposed by the present writer in 1927 (Stensiö 1927, pp. 38–40), there is in the Cephalaspids a mucous canal system homologous to that of the Tremataspids with which it agrees in essential features (*cf.* STENSIÖ 1927, pp. 38–40, Pl. 72, figs. 1, 2). As this canal system is found both in the Cephalaspids and in the Tremataspids we are, of course, led to the conclusion that it was already present in their common ancestors, and that it must have originated early among the *Osteostraci*, or probably even in their ancestors (*cf.* the account of the *Heterostraci* below). It is also obvious that the mucous canal system in the Cephalaspids is subject to considerable variation, not only with regard to its position in relation to the exoskeleton, but also in certain details in its development and arrangement.



TEXT-FIG. 7.—*Hemicyclaspis murchisoni* (EGERTON). Transverse section through the exoskeleton of the cephalic shield. The section shows clearly the relations between the mucous canal system and the vascular canals. Owing to the fact that the section is taken from a part of the cephalic shield situated rather close to the rostral margin, the middle layer is very thick and the course of the radiating canals complicated. Section made from specimen no. P.14012 in the British Museum. Approx. × 150 diam.

ebc, external branches from the radiating canals (these branches form the sub-epidermal vascular plexus); *ita*, intra-areal mucous canals; *ml*, middle layer (basal parts not shown); *p*, pores by means of which the mucous canals open outwards; *rad.c*, radiating canals; *sl*, superficial layer.

The mucous canal system is not only confined to the cephalic shield, but also occurs throughout the trunk and on the pectoral fins (*cf.* the chapters on the microstructure of the scales and on the pectoral fins). For further details concerning this canal system and for opinions concerning its function the reader is referred to the chapter on the mucous canal system below.

We will now turn to the vascular canals of the exoskeleton. In the Spitsbergen forms I was able to show (STENSIÖ 1927, pp. 34, 35, 36) that the exoskeleton is rich in vascular canals, and that these canals are arranged in certain distinct groups which in their extent coincide with the polygonal areas. Now since we know that the subdivision of the exoskeleton of the cephalic shield into polygonal areas is due to the mucous canal system, it follows that the arrangement of the vascular canals into groups—vascular areas—is also determined by the mucous canal system, which is thus a dominant factor in the structure of the exoskeleton.

The vascular canals of the exoskeleton of the British forms could in certain respects be studied in greater detail than those of the Spitsbergen forms, and hence it will be necessary to give a fairly detailed account of them here.

The sub-aponeurotic (sub-cutaneous) vascular plexus (*dplx*, text-fig. 6; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 32, fig. 6; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62; Pl. 64, figs. 2, 3) is as well developed as in the Spitsbergen forms and, as in them, it lies partly beneath and partly in the deepest parts of the basal layer of the exoskeleton. From this plexus the ascending vascular canals (*c.asc*, Pl. 36, figs. 1, 2; Pl. 41, figs. 1, 2; Pl. 44, figs. 1–3; Pl. 45, fig. 3; Pl. 58, figs. 2, 3; Pl. 59, figs. 3–5; Pl. 63; Pl. 64, figs. 2, 3; Pl. 65, figs. 1–3; Pl. 66, figs. 1, 2), which in *H. murchisoni* and often in *C. salweyi* are very wide basally, issue in groups, each of which corresponds to a polygonal area, and the canals of each such group also enter and perforate the basal layer of their polygonal area in a more or less pronounced centripetal direction, passing up to the middle layer, just as in the Spitsbergen forms. As the various canals in each group give off no branches, or only very few, to the basal layer, this layer in all forms was very poorly supplied with vessels. On reaching the middle layer, each group of ascending vascular canals breaks up in the centre of their polygonal area into a number of irregular canals, which then towards the periphery merge into the radiating canals (*rad.c*, text-figs. 6, 7; Pl. 4, fig. 3; Pl. 10, figs. 1–3; Pl. 13, figs. 1, 2; Pl. 24, fig. 2; Pl. 26, fig. 2; Pl. 27, fig. 1; Pl. 29, fig. 1; Pl. 32, figs. 1–3; Pl. 36, figs. 1, 2, 4; Pl. 41, figs. 1–2; Pl. 44, figs. 1–3; Pl. 45, figs. 2, 3; Pl. 56, figs. 2, 3; Pl. 57, fig. 2; Pl. 58, figs. 2, 3; Pl. 59, figs. 3–5; Pl. 60, figs. 1–4; Pl. 63, figs. 1–3; Pl. 64, figs. 1–3; Pl. 66, fig. 1). The latter are well developed and in all respects like those in the Spitsbergen forms: they are situated exclusively in the most basal parts of the middle layer and radiate from the central parts of each polygonal area towards the borders, where they are continuous with, and pass directly over into, the corresponding canals of the adjacent polygonal areas. Furthermore, the radiating canals branch during their course from the central part of each polygonal area, so that they are most numerous at the borders; and they are usually arranged in distinct fascicles which correspond in number to the sides of the polygonal area in which they are situated. Just where they unite with those of the neighbouring areas these canals curve inwards, so that they lie deeper there than elsewhere; a fact which explains why they are often to be seen at the margins of these areas, even when the exoskeleton is much weathered. Finally, it should be mentioned that the radiating canals are in communication with each other by means of short transverse branches.

From the superficial side of the radiating canals numerous external branches pass into the outermost parts of the middle layer (*ebc*, text-figs. 6, 7; Pl. 10, fig. 1;

Pl. 29, fig. 1; Pl. 32, fig. 4; Pl. 44, fig. 1; Pl. 45, fig. 3; Pl. 57, fig. 2; Pl. 59, fig. 3; Pl. 60, figs. 2–4; Pl. 63, figs. 2, 3; Pl. 64, figs. 2, 3; Pl. 66, fig. 1), forming a complex network with each other, exactly as in the Spitsbergen forms: this network I termed the *sub-epidermal vascular plexus.* When I examined the Spitsbergen Cephalaspids I thought that these branches perforated the superficial layer, but, as already pointed out (p. 19), the British forms show quite clearly that this is not the case, and instead we find that the branches in question go partly to the mucous canals and partly to the outermost part of the middle layer between the mucous canals. Here, between the mucous canals, they break up into very fine branches from which the dentine-canals of the superficial layer issue (text-fig. 7; Pl. 60, figs. 2–4; Pl. 63, figs. 2, 3; Pl. 64, fig. 1; Pl. 66, fig. 1). In those forms in which the superficial parts of the exoskeleton are present only as isolated tubercles on the middle layer, the canals of the sub-epidermal vascular plexus are found only in the tubercles themselves (Pl. 66, fig. 1), for between the tubercles they were situated entirely in soft tissue.

In addition to those described above, other kinds of vascular canals could be observed in the exoskeleton of the cephalic shield. Thus in several of the British forms where the radiating canals of one area pass over into those of the adjacent areas, there occur numbers of rather fine canals, which descend through the basal layer to the sub-aponeurotic (sub-cutaneous) vascular plexus. These canals, which we may term the *descending vascular canals* (*c.des*, Pl. 41, figs. 1, 2; Pl. 58, fig. 2; *a*, Pl. 59, figs. 4, 5), lie immediately beneath the inter-areal mucous canals or grooves, and accordingly have a strictly inter-areal position in the basal layer. In *Cephalaspis salweyi*, *C. powriei* and certain other species they do not open directly downwards into the sub-aponeurotic vascular plexus, but into ring-shaped canals or cavities, the ring-sinuses, which lie directly beneath the inter-areal mucous canals or grooves. These ring-sinuses have already been observed and figured in *C. salweyi* by LANKESTER (1870, Pl. 14, fig. 7). In this species they lie partly in, and partly beneath, the bottom-most laminae of the basal layer, and are very well developed (*r.sin*, Pl. 11, fig. 4; Pl. 12, fig. 2; Pl. 36, figs. 1, 2; Pl. 59, figs. 4, 5). In *C. powriei*, on the contrary, they are situated entirely in the basal layer, but they are there usually much more imperfectly developed than in *C. salweyi* (*r.sin*, Pl. 41, figs. 1, 2; Pl. 44, figs. 2, 3; Pl. 58, fig. 2). In these and other instances in which they occur, the basal layer, as a result of their presence, becomes subdivided into areas, which correspond in their extent exactly to the polygonal areas bounded by the inter-areal mucous grooves or canals. Both the descending vascular canals and the ring-sinuses naturally weaken the basal layer beneath the inter-areal mucous grooves or canals, and therefore this layer is often in the fossil condition fractured there, giving one the impression that the exoskeleton was subdivided into very definite and independent polygonal areas throughout its thickness.

On account of their generally narrow diameter and straight course, the ascending vascular canals have the appearance of arterial canals, and it seems therefore likely that the vessels lodged in them carried blood from the sub-aponeurotic vascular plexus to the exoskeleton. On the other hand, the ring-sinuses, which are strikingly wide, can hardly have lodged anything else than veins, and the fact that the descending vascular canals open into these sinuses suggests that these canals transmitted veins through which the blood was returned to the veins of the sub-aponeurotic vascular plexus. If this interpretation of the ascending and descending vascular canals is correct, the blood supply of the exoskeleton must thus have been effected in the following way: from the sub-aponeurotic vascular plexus, or more correctly from the arteries or more arterial parts of this plexus, the blood passed first outwards into the exoskeleton through the supposed arteries in the ascending vascular canals, and from these further outwards through the radiating canals and the sub-epidermal vascular plexus, which supplied the mucous canal system, the most external parts of the exoskeleton, and indirectly also, the basal part of the epidermis. In the sub-epidermal plexus the blood probably did not stream in any definite direction, since there was no direct draining of this plexus, but it seems only to have passed out again therefrom into the radiating canals, from which part of it at least then flowed downwards into the descending canals and the ring-sinuses, finally emptying into the veins of the more or less venous parts of the sub-aponeurotic vascular plexus.[1]

Sclerodus [*Eukeraspis*] *pustuliferus* differs considerably from the other Cephalaspids with regard to this vascular canal system in that it has no radiating canals and its vascular canals exhibit no traces of any arrangement in vascular areas. The explanation of this very striking feature may lie, as suggested above, in the complete absence of the mucous canal system in this species.

In this connection a brief account must be given of the polygonal plates which cover the electric fields. These plates are well displayed in several of the British species (Pl. 1, figs. 1–3; Pl. 2, figs. 1, 4; Pl. 3, figs. 1, 4; Pl. 4, figs. 1, 2; Pl. 5, figs. 3–6; Pl. 6, figs. 1, 2; Pl. 7, fig. 4; Pl. 28, fig. 3; Pl. 30, figs. 1, 3; Pl. 31; Pl. 36, figs. 3, 4; Pl. 37, fig. 3; Pl. 38, figs. 3, 4; Pl. 39, figs. 1, 2; Pl. 40, fig. 1; Pl. 43, figs. 1, 2), but are best preserved in *Hemicyclaspis murchisoni* and in *Cephalaspis pagei*, in which they may lie very close to each other, in *H. murchisoni* so close that from the outside their outlines are hardly discernible (Pl. 5, fig. 6). In both *H. murchisoni* and *C. pagei* it is very clearly seen that they consist of the same three layers as the rest of the exoskeleton (Pl. 5, fig. 6), and that accordingly they represent the exoskeleton in its entire thickness and not only the outermost portion. In *H. murchisoni* the superficial parts of the plates are always completely developed and continuous, but in *C. pagei* this is the case only in certain specimens, for in other specimens these parts are present in isolated tubercles only. It is thus obvious that the development of the outer parts of these plates is in keeping with that of the rest of the exoskeleton of the cephalic shield. Further, it is evident that in *H. murchisoni* and *C. pagei* every one of these plates developed as a single polygonal unit of the exoskeleton of the cephalic shield, each with its own group of ascending vascular canals which breaks up into fascicles of radiating vascular canals (*rad.c*), giving off in their turn external branches in the usual way. Finally, it is clear that in both species each of the plates was also independent in its relations to the mucous canal system. Thus the inter-areal canals probably lay between or in the peripheral parts of the plates, whereas the intra-areal canals lay either within or superficially to the plates. It seems very unlikely that these plates in other Cephalaspids differed fundamentally from those of *H. murchisoni* and *C. pagei*.

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[1] In several of the vascular canals there was in addition to the vessels a little uncalcified connective tissue.

In this chapter we have seen that the exoskeleton in a great many Cephalaspids has its superficial parts continuous, *i.e.* developed so that they form a continuous covering to the layers situated more basally, and, as is well known, the exoskeleton in *Tremataspis* is always developed in this manner. As it does not seem likely that this development of the exoskeleton can have arisen independently in a great number of Cephalaspids and in the Tremataspids, there is evidently good reason to suppose that it was inherited from their common ancestors, *i.e.* from the most primitive *Osteostraci*. In the Spitsbergen Cephalaspids the superficial parts of the exoskeleton are more completely developed in the Downtonian than in the Devonian forms, a condition which is of great interest to us here, as it shows that these parts of the exoskeleton of the Cephalaspids were not in a progressive but in a regressive state of development. There are thus facts which indicate that the exoskeleton of the cephalic shield of the Cephalaspids is more primitive in character when its superficial parts are completely developed and form a continuous covering to the basal layers than when these parts are present only in isolated tubercles. The latter condition is the result of regressive development of the exoskeleton. That the exoskeleton in the British Cephalaspids is subject to such great variations in its superficial parts, not only in different species but even in different individuals of the same species, is in full accordance with the view that the exoskeleton in general of the Cephalaspids is in a regressive state of development.

It is interesting to note that also in several groups of the more primitive fishes a regressive development of the exoskeleton took place in a similar way to that in the Cephalaspids, inasmuch as the superficial layer, which in them consists of cosmine or ganoine, suffered reduction (*cf.* STENSIÖ 1925*a*, pp. 161–164).

Finally, we turn to the description of the endoskeleton. As mentioned in a previous chapter (pp. 10–13), this was not completely ossified in any of the British forms; indeed, in some it was almost entirely cartilaginous. Its perichondrial bone-layers, which in most cases are very thin, are continuous with and grade into the basal layer of the exoskeleton, as in the Spitsbergen forms, with which they also agree in their micro-structure (STENSIÖ 1927, pp. 40–41).

Since, as in the Spitsbergen species, the proximal part of the basal layer of the exoskeleton is intimately related to the endoskeletal structures underneath it, it is conceivable that this layer may include certain laminae formed by the perichondrium of the underlying endoskeleton, and may therefore be of endoskeletal origin (*cf.* STENSIÖ 1927, pp. 40–41).

Oralo-branchial chamber and post-branchial wall.—In form the oralo-branchial chamber is similar to that in the Spitsbergen forms (STENSIÖ 1927, pp. 41–47). It should be noticed, however, that the part of the external perichondrial bone-layer which lines its walls is generally very thin and imperfectly developed (Pl. 8, fig. 4; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 1). The aortic ridge (*r.aort*, Pl. 14, figs. 5–7; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 1; Pl. 28, figs. 1, 2; Pl. 37, fig. 1; Pl. 49, fig. 3; Pl. 53, fig. 5) and the orbital and otic prominences (*pr.orb, pr.au*, Pl. 8, fig. 4; Pl. 14, figs. 5, 7; Pl. 19, fig. 3; Pl. 25, figs. 1, 2; Pl. 28, figs. 1, 2; Pl. 32, fig. 5; Pl. 37, fig. 1; Pl. 49, fig. 3; Pl. 53, fig. 5) are to be seen in certain specimens, mostly, however, as impressions only. The area which formed the upper boundary of the mouth, and which therefore may be called the *supra-oral field* (*dpr*, Pl. 8, fig. 4; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 1; Pl. 28, fig. 1; Pl. 54, figs. 1–4; Pl. 55, fig. 1), is fairly often preserved, when it is clearly seen to vary somewhat in shape and size in different species. It is best shown in *Cephalaspis salweyi* in which its surface is somewhat rough (Pl. 25, fig. 1). In *Didymaspis grindrodi* (Pl. 54, fig. 2) and *Hemicyclaspis murchisoni* (Pl. 8, fig. 4) it is, as in *Thyestes verrucosus, Micraspis gracilis* and *Tremataspis* (*cf.* Stensiö 1927, p. 150; and Kiaer 1928, pp. 127–129), provided with small, tooth-like tubercles. In *D. grindrodi* these tooth-like tubercles occur throughout its extent, whereas in *H. murchisoni* they are found on a narrow median portion only. The branchial fossae are partly preserved in *Hemicyclaspis murchisoni, Cephalaspis salweyi, C. pagei, C. langi, Benneviaspis anglica, Thyestes egertoni* and *Didymaspis grindrodi* (*k*, k_1–k_{10}, Pl. 6, figs. 1–3; Pl. 8, fig. 4; Pl. 11, fig. 1; Pl. 25, fig. 1; Pl. 52, figs. 3, 4; Pl. 54, figs. 1, 2; Pl. 55, fig. 2), and as far as can be judged they are 10 in number in each case, suggesting that this number is constant for all typical Cephalaspids. In *Tremataspis* also the same number of branchial fossae seems to be present.

The post-branchial wall is displayed more or less clearly in a few of the forms (*p.brw*, Pl. 8, fig. 4; Pl. 32, fig. 5; Pl. 52, fig. 4; Pl. 53, fig. 5).

DESCRIPTION OF THE DIFFERENT PARTS OF THE CEPHALIC SHIELD

Cephalic Division Proper

Since in both general features and anatomical details the cephalic division proper of the cephalic shield is like that of the Spitsbergen forms, it is not necessary to give a complete account of it here. The following description will therefore be chiefly confined to an enumeration of the most important anatomical details to be seen in the various forms. For a full account of the anatomy of this division the reader is referred to my monograph on the Spitsbergen Cephalaspids (Stensiö 1927, pp. 47–245).

Endocranium

The endocranium is similar in shape and extent to those of the Spitsbergen forms and, as pointed out, it is likewise continuous with the dorsal division of the visceral endoskeleton, the endoskeletal shoulder-girdle, and the pronephros component. As has also been mentioned (pp. 10–13), it consisted of cartilage lined with perichondrial bone-layers, which in the Downtonian forms are generally stronger and more completely developed than in most of those of Devonian age.

Occipital region.—In *Sclerodus* [*Eukeraspis*] the occipital region is not preserved, but as far as can be judged it was probably very short. In all the other British Cephalaspids it is well developed and, as in the Spitsbergen Cephalaspids, it varies in length according to the extension caudally of the exoskeleton of the inter-zonal part: it ends as a rule in front of the posterior margin or the posterior angle of the inter-zonal exoskeleton, although in certain species it may have reached further. Its lateral boundaries are displayed in several species (text-figs. 3, 4, 61; *otl*, Pl. 26, fig. 1; Pl. 35, fig. 1; Pl. 38, fig. 2; Pl. 50, figs. 2–4; Pl. 51, figs. 1, 2, 5; Pl. 52, figs. 2, 3; Pl. 54, fig. 4; Pl. 55, fig. 1).

The dorsal surface of the region is occupied in its median part by the most posterior portion of the dorsal electric field. The paired canal which was denoted by d_1 in the Spitsbergen forms is also present in the British specimens, and, as previously noted (Stensiö 1927, pp. 61–62, 85–86, fig. 83), this canal probably lodged the ductus endolymphaticus, and in those species in which it opens into the dorsal electric field, possibly also a vein from that field. In *Thyestes egertoni* and *Didymaspis grindrodi* its dorsal opening is situated at the postero-lateral angle of the dorsal electric field (d_1, text-figs. 60, 61; Pl. 27, figs. 3, 4; Pl. 40, fig. 2; Pl. 50, fig. 3; Pl. 51, fig. 2; Pl. 54, figs. 1–3; Pl. 55, figs. 3, 4). In *Sclerodus* [*Eukeraspis*] *pustuliferus* nothing concerning it is so far known. In all the other British forms it opens dorsally into the dorsal electric field slightly in front of the posterior end, just as in the Cephalaspids from Spitsbergen (d_1, Pl. 13, fig. 2; Pl. 15, fig. 2; Pl. 21; Pl. 30, fig. 2; Pl. 35, figs. 1, 2; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2).

The ventral surface of the region is not exposed in any specimen. In *Didymaspis*, however, we find on the ventral surface of the inter-zonal exoskeleton, and laterally to the posterior part of the region, a very pronounced groove (*a.gr*, Pl. 54, figs. 3, 4; Pl. 55, figs. 1, 3, 4) which shows that, as in *Kiaeraspis* and *Hoelaspis*, the aorta as far back as this part lay decidedly to the right of the median line.

No other details of importance are to be seen in this region.

Otic region.—The otic region is badly preserved in all the British Cephalaspids, but it is nevertheless clear that both in its proportions and general relations it must have been as in the Spitsbergen species.

Its dorsal surface is as a rule well preserved. On this surface we find medially a portion of the dorsal electric field, and on each side of this several canals, both of the vascular and nervous systems.

Usually the ventral surface is available for study only as an imperfect impression. It is of special interest that in *Sclerodus* [*Eukeraspis*] *pustuliferus* it is developed in a way similar to that in the other Cephalaspids; thus it has (Pl. 53, fig. 5) a distinct otic prominence (*pr.au*), bounded anteriorly by a pronounced orbito-otic groove (*orb.ot.gr*), and an aortic ridge (*r.aort*) with a deep aortic groove (*aort.gr*), which towards the occipital region gradually changes its position from truly median to the right side of the median line, and at the transition between the otic and occipital regions is bridged over ventrally by the post-branchial wall (*p.brw*).

The division of the cavum cerebrale which falls within the region is to be seen only in *Securiaspis, Thyestes, Didymaspis* and *Sclerodus* [*Eukeraspis*], in which it is provided with a well-developed lining of perichondrial bone. In *Securiaspis kitchini* and *Thyestes salteri* the part that lodged the metencephalon (*met,* Pl. 50, figs. 1, 4) is displayed, whereas in *Didymaspis* and *Sclerodus* [*Eukeraspis*] the part that lodged the medulla oblongata (*med,* Pl. 52, fig. 2; Pl. 54, fig. 4) is exposed instead. This division of the cavum is so imperfectly preserved that no details can be discerned, but despite this it is fully evident that its general shape must have been very much like that in *Kiaeraspis* and *Hoelaspis* from the Spitsbergen Downtonian.

The nerve canals of the region, with the exception of those of the lateral electric fields, are very imperfectly known owing to the fact that their perichondrial bone-layers in the majority of the species were very delicate, or perhaps even entirely absent. The wide acustico-facialis canal could be observed only in *Cephalaspis salweyi* and a few other species; likewise the canals which transmitted the n. facialis and the n. glossopharyngeus from the labyrinth cavity to the oralo-branchial chamber are to be seen but rarely, the n. facialis canal being shown in *C. salweyi, Benneviaspis anglica, Securiaspis kitchini* and *Sclerodus* [*Eukeraspis*] *pustuliferus* (*VII,* text-figs. 10, 13; Pl. 25, fig. 2; Pl. 48, fig. 2; Pl. 49, fig. 1; Pl. 51, fig. 2; Pl. 52, fig. 2; Pl. 53, fig. 5) and the n. glossopharyngeus only in *C. salweyi* (*IXa,* Pl. 25, fig. 1). The canal of the nerve of the dorsal electric field has been found in *C. salweyi, Thyestes salteri, Sclerodus* [*Eukeraspis*] *pustuliferus* and *Didymaspis grindrodi,* but in most of these species it is imperfectly exposed (*des,* Pl. 25, fig. 1; Pl. 50, fig. 2; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2; Pl. 54, figs. 1–3; Pl. 55, figs. 3, 4). Finally, the nerve canals of the lateral electric fields are more or less completely shown in a great number of species ($sel_{1,2}$–sel_6, text-figs. 9–13; Pl. 4, fig. 4; Pl. 14, fig. 7; Pl. 15, fig. 1; Pl. 18, figs. 5, 6; Pl. 19, figs. 1, 2; Pl. 23, figs. 2, 3; Pl. 25, figs. 1, 2; Pl. 26, fig. 1; Pl. 49, figs. 1, 3; Pl. 50, figs. 1–4; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1), but their most proximal parts could be studied only in a specimen of *C. salweyi* (Pl. 25, fig. 1). A more detailed account of all the nerve canals of the electric fields will be given below.

The vascular canals of the region are fairly completely preserved, especially in *Benneviaspis* and *Securiaspis,* and in some species of *Cephalaspis,* such as *C. whitei* and *C. powriei.* In these species the canals of the dorso-lateral superficial arteries (*a.la, a.sa,* $a.sm_1$, $a.sm_2$, *a.sp, a.slcm,* text-figs. 9, 10, 11, 12; Pl. 18, fig. 6; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62) and the canals of the dorso-lateral superficial veins 3–6 ($v.ls_{3\text{-}6}$, Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pl. 50, fig. 3; Pl. 51, fig. 2; Pls. 61, 62) are well shown, and in addition in *Thyestes,* in *Didymaspis,* in *Sclerodus* and exceptionally also in *Cephalaspis* the canal of the post-orbital division of the v. capitis lateralis (*v.cl,* text-fig. 13; Pl. 50, figs. 2, 3; Pl. 51, figs. 1, 2; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1).

Labyrinth cavity.—The labyrinth cavity has so far been found in *Sclerodus* [*Eukeraspis*], *Didymaspis, Thyestes, Hemicyclaspis murchisoni* and a few species of *Cephalaspis,* in all of which it is more or less completely lined by a perichondrial bone-layer—the labyrinth bone-layer—and it is very likely that this layer was also present in *Securiaspis* and *Benneviaspis,* although it has not as yet been clearly observed. In most species of *Cephalaspis,* however, it was probably very imperfectly lined or perhaps not at all, and thus nothing of it has been preserved in these species.

It is clear that the labyrinth cavity is in all essentials as in the Spitsbergen forms. Thus we may distinguish a vestibular division (*vest,* Pl. 24, fig. 1; Pl. 25, fig. 1; Pl. 50, fig. 4), well exposed in an indeterminable species of *Cephalaspis* and in *Cephalaspis salweyi*; a commissural division (*com,* text-fig. 13; Pl. 50, figs. 2, 3; Pl. 51, figs. 1, 2; Pl. 52, fig. 2), which is displayed in *Thyestes* and in *Sclerodus* [*Eukeraspis*]; and divisions for the anterior and posterior semicircular canals (*c.sem.ant, c.sem.post,* text-fig. 13; Pl. 5, fig. 5; Pl. 22, fig. 5; Pl. 25, fig. 1; Pl. 50, figs. 2, 3; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2; Pl. 54, fig. 4), well shown in *Hemicyclaspis murchisoni, Cephalaspis salweyi, Thyestes* and *Sclerodus* [*Eukeraspis*].

The canals of the six nerves of the lateral electric field issue from the vestibular division of the labyrinth cavity in a way similar to those in the Spitsbergen forms, whose canals they resemble in most respects ($sel_{1,2}$, sel_1–sel_6, text-figs. 9–13; Pl. 1, figs. 2, 3; Pl. 4, fig. 4; Pl. 5, fig. 2; Pl. 7, fig. 4; Pl. 14, figs. 1, 2, 7; Pl. 15, figs. 1, 5; Pl. 16, figs. 3, 4; Pl. 17, fig. 2; Pl. 18, figs. 2, 5, 6; Pl. 19, figs. 1–3; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 23, figs. 2, 3; Pl. 25, fig. 2; Pl. 26, fig. 1; Pl. 28, fig. 2; Pl. 35, figs. 1, 2; Pl. 38, figs. 1, 2; Pl. 47, fig. 1; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 3; Pl. 50, figs. 1–4; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1; Pls. 61, 62). Thus they are five in number at the exit from the labyrinth cavity, but the most anterior ($sel_{1,2}$), which lodged the two most anterior nerves, bifurcates in most of the forms at a varying distance from the labyrinth cavity: in *Hemicyclaspis* and *Cephalaspis,* with the exception of *C. powriei* and its varieties, its bifurcation takes place at the antero-lateral corner of the orbital opening (Pl. 1, figs. 2, 3; Pl. 8, fig. 4; Pl. 14, figs. 2, 7; Pl. 15, figs. 1, 5; Pl. 18, figs. 5, 6; Pl. 19, fig. 2; Pl. 22, fig. 5; Pl. 23, figs. 2, 3; Pl. 25, fig. 2; Pl. 38, figs. 1, 2); in *C. powriei* and its varieties it bifurcates even somewhat later (Pl. 26, fig. 1), and in *Benneviaspis* and *Securiaspis* about midway between the antero-lateral corner of the orbital opening and the lateral electric field (Pl. 47, fig. 1; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 3; Pl. 50, fig. 1); finally, in *Thyestes, Sclerodus* [*Eukeraspis*] and probably also in *Didymaspis,* as in *Boreaspis* and *Kiaeraspis* from the Spitsbergen Downtonian, it does not bifurcate until just before, or even at, its entrance into the lateral electric field (Pl. 50, figs. 2–4; Pl. 51, figs. 1, 2, 5.; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1).

The canal of the nerve of the dorsal electric field is to be seen in a more or less imperfect state of preservation in several species. Usually only its entrance into the dorsal electric field or its branches in that field are conspicuous (*des,* Pl. 12, fig. 1; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 2; Pl. 27, fig. 2; Pl. 30, fig. 2; Pl. 35, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 50, figs. 2, 3; Pl. 51, figs. 1, 2, 5; Pl. 54, figs. 1–3; Pl. 55, figs. 3, 4), but in *Sclerodus* [*Eukeraspis*] and in *C. salweyi* it is exposed up to its origin from the labyrinth cavity (*des*, Pl. 25, fig. 1; Pl. 52, fig. 2).

As we have already noted in the description of the otic region, in addition to these nerve canals there are in a few instances remains of the canals through which the n. glossopharyngeus and the n. facialis left the labyrinth cavity and passed to the oralo-branchial chamber (*VII*, text-figs. 10, 13: *VII*, *IXa*, Pl. 25, figs. 1, 2; Pl. 48, fig. 2; Pl. 51, fig. 2; Pl. 52, fig. 2; Pl. 53, fig. 5).

Finally, the canals of the dorso-lateral superficial arteries (*a.la*, *a.sa*, *a.sm*$_1$, *a.sm*$_2$, *a.slcm*, *a.sp*, text-figs. 9–12; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2) seem to have issued from the labyrinth cavity essentially as in the Spitsbergen forms. The most proximal parts of these canals, however, are not preserved in any of the species.

Orbito-temporal region.—The orbito-temporal region is imperfectly preserved in most of the English Cephalaspids, but it is evident that in general shape and relations it did not differ from that in the Spitsbergen forms.

The dorsal surface is often fairly well exposed. On it there is, as we have already seen (*cf.* pp. 4–5), the pineal depression (*pd*, text-fig. 1; Pl. 4, fig. 4; Pl. 13, fig. 2; Pl. 15, figs. 2, 3; Pl. 16, fig. 2; Pl. 18, figs. 2, 3; Pl. 23, figs. 2, 3; Pl. 54, figs. 1–3; Pls. 61, 62), in which the ventral division of the pineal canal, that is the division of the pineal canal which perforates the endoskeleton, has its dorsal opening (*pin*$_1$, text-fig. 1; Pl. 4, fig. 4; Pl. 13, fig. 2; Pl. 14, fig. 1; Pl. 15, figs. 2, 3; Pl. 16, fig. 3; Pl. 18, figs. 2, 3, 6; Pl. 19, figs. 1, 2; Pl. 23, figs. 2, 3; Pl. 24; Pl. 26, fig. 2; Pl. 27, figs. 3, 4; Pl. 35, figs. 1, 2; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pl. 50, fig. 2; Pl. 51, figs. 1, 2; Pl. 54, figs. 1–4; Pl. 55, figs. 1, 3, 4; Pls. 61, 62). The other division of the pineal canal (*pin*$_2$) is, as we have seen (pp. 4–5), situated entirely in the pineal plate (*Ppl*). Close behind the pineal depression follows the dorsal electric field (*dsf*), which continues backwards on the dorsal surface of the otic region and so for some distance on the dorsal surface of the occipital region. Laterally to the dorsal electric field and the orbital opening on each side, we usually find in this region several nerve- and vascular canals preserved.

The ventral surface of the orbito-temporal region is much more imperfectly known than the dorsal. On it there is normally the well-developed orbito-temporal division of the aortic ridge (*r.aort*, Pl. 25, fig. 1; Pl. 28, fig. 1; Pl. 49, fig. 3; Pl. 53, fig. 5) and on each side of this an orbital prominence (*pr.orb*, Pl. 8, fig. 4; Pl. 14, figs. 5, 7; Pl. 25, figs. 1, 2; Pl. 28, figs. 1, 2; Pl. 32, fig. 5; Pl. 37, fig. 1; Pl. 49, fig. 3; Pl. 53, fig. 5), which is always well defined. As in the Spitsbergen forms, this prominence is bounded posteriorly by the orbito-otic groove (*orb.ot.gr*, Pl. 53, fig. 5) and anteriorly by the sub-nasal fossa, which is usually fairly deep (*f.sn*, Pl. 53, fig. 5). Postero-laterally to this fossa in *C. salweyi* there are remains of the inter-branchial ridge 3 (Pl. 25, fig. 1). It is especially worthy of notice that the orbito-temporal surface is developed in *Sclerodus* [*Eukeraspis*] in an essentially similar way to that in the other Cephalaspids.

The orbit is probably lined in all forms by a continuous perichondrial bone-layer, the orbital bone-layer, but despite this it is always so imperfectly preserved that very little detail can be seen. It is quite evident, however, that in all features of any importance it must have been as in the various Cephalaspids from Spitsbergen.

From the size of the orbit it is evident that the eye was as a rule large and well developed. In *Hemicyclaspis murchisoni*, *Cephalaspis pagei* and *C. spinifer* it was provided with a sclerotic ossification (*sclr*, text-figs. 15, 23, 25, 33A; Pl. 1, figs. 1–3; Pl. 2, fig. 4; Pl. 3, figs. 1, 4; Pl. 4, fig. 2; Pl. 5, figs. 3, 5; Pl. 7, fig. 4; Pl. 22, fig. 5; Pl. 38, figs. 3, 4; Pl. 39; Pl. 42, figs. 1, 2; Pl. 46, figs. 1, 2), which in *Hemicyclaspis murchisoni* is a continuous ring of bone, but in *Cephalaspis pagei*, *C. spinifer* and certain other species, on the contrary, it is much less developed, being usually represented only by a dorsal part, which is ornamented externally with tubercles similar to those on the exoskeleton of the cephalic shield.

The orbito-temporal division of the cavum cerebrale cranii is found to be lined by a more or less complete perichondrial bone-layer in *Hemicyclaspis murchisoni* (Pl. 8, fig. 4), in certain species of *Cephalaspis*, such as *C. salweyi* (Pl. 25, fig. 1), in *Securiaspis* (Pl. 50, fig. 1), in *Sclerodus* [*Eukeraspis*] *pustuliferus* (Pl. 52, fig. 2; Pl. 53, fig. 5) and also in *Didymaspis grindrodi* (Pl. 54, fig. 4). In none of these forms, however, is it so well preserved as to exhibit many details. There is, however, enough of it to show that in all main features it must have been similar to that in the Spitsbergen forms.

In *Sclerodus* [*Eukeraspis*] (Pl. 52, fig. 2) there was a wide fenestra optica, exactly as in the Spitsbergen species, and it seems that this was similarly developed in all the other British Cephalaspids. The canals through which the n. oculomotorius and the n. trochlearis left the cavum cerebrale cranii and reached the orbit could not be observed in any of the British specimens, but it cannot be doubted that both these canals were present and that their course was as in the Spitsbergen forms. The canal through which the roots, at least, of the n. trigeminus proper had their exit from the cavum cerebrale to the orbit is to be seen in a fragmentary condition in *C. salweyi* only. We thus find that the nerve canals which issue from the cavum cerebrale in this region are all either imperfect or not preserved at all. On the other hand the canals through which the n. profundus and the n. trigeminus proper left the orbit and passed down to the oralo-branchial chamber are preserved rather more frequently (V_1, V_2, text-figs. 9, 10, 12, 13; Pl. 4, fig. 4; Pl. 14, fig. 2; Pl. 18, fig. 6; Pl. 19, fig. 1; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, figs. 1, 3, 4; Pl. 51, fig. 2; Pl. 52, fig. 2). The canal most often found in the region is, however, the common canal of the two most anterior nerves of the lateral electric field. This canal passes laterally close to the orbit in *Hemicyclaspis*, *Cephalaspis*, except *C. powriei*, in *Benneviaspis* and *Securiaspis*, just as in the Spitsbergen forms ($sel_{1,2}$, text-figs. 10, 12; Pl. 18, fig. 5; Pl. 22, fig. 5; Pl. 48, fig. 2; Pl. 49, figs. 1, 3; Pl. 50, fig. 1), whereas in *Cephalaspis powriei*, *Thyestes*, *Sclerodus* [*Eukeraspis*] and *Didymaspis* (text-fig. 13; Pl. 26, fig. 1; Pl. 50, figs. 2–4; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2;

Pl. 54, fig. 4; Pl. 55, fig. 1) its course lies somewhat below and postero-laterally to the orbit.

The canal of the a. carotis interna is fairly well displayed in several of the species (*a.car*, Pl. 25, fig. 1; Pl. 53, fig. 5), and it is clear that it perforates the floor of the cavum cerebrale cranii much as in the Spitsbergen forms. Several of the branches of the canal of the a. facialis (*a.fac*) are not infrequently preserved in this region, and of these the lateral and medial infra-orbital branches may be specially mentioned (*a.iol, a.iom*, text-figs. 9–12; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 2; Pls. 61, 62). These two branches appear to be as in the Spitsbergen forms in all important features, so that it is evident that the branching of the a. facialis must have been fairly constant in all Cephalaspids.

Both the canal of the dorso-lateral superficial vein 3 and the canal of the pre-orbital division of the v. capitis lateralis are preserved in several instances. In the British species of *Cephalaspis*, the former ($v.ls_3$, text-figs. 9–13; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 2; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pl. 50, figs. 3, 4; Pl. 51, fig. 2; Pls. 61, 62) runs as a rule up to, and opens in, the most posterior part of the orbit, as in the species from Spitsbergen, and it seems not unlikely that this is also the case in *Hemicyclaspis*. In *Securiaspis*, *Benneviaspis* and *Thyestes*, on the contrary, it always turns further backwards and runs either directly to the post-orbital division of the canal of the v. capitis lateralis, or unites with the canal of the dorso-lateral superficial vein 4, through which its blood in this case was brought to the post-orbital division of the v. capitis lateralis. It is of interest to note that the canal of this dorso-lateral superficial vein 3 also opened into the canal of the v. capitis lateralis posteriorly to the orbit in *Benneviaspis holtedahli*, *Hoelaspis* and *Kiaeraspis* from Spitsbergen; and accordingly this connection must be regarded as characteristic of the genera *Securiaspis*, *Benneviaspis*, *Hoelaspis*, *Thyestes* and *Kiaeraspis*, and, we may expect also, of *Boreaspis* and *Didymaspis*.

The canal of the pre-orbital division of the v. capitis lateralis ($v.\ cl_1$, text-figs. 9–13; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 48, figs. 1, 2; Pl. 51, fig. 2) is often seen in a fair state of preservation. It has its normal position and opens into the orbit as in the Spitsbergen Cephalaspids. Its course and branches will be dealt with in greater detail in the following account of the ethmoidal region.

Ethmoidal region.—In both shape and relations to the orbito-temporal region and the dorsal division of the visceral endoskeleton, the ethmoidal region is in all essentials as in the Spitsbergen forms.

The dorsal surface is well exposed in several species. On the median part of this surface lies, as is usual, the naso-hypophysial aperture, and it is of interest to find that the anterior division of this aperture (na_1), that is, the division forming the external opening of the hypophysial sac, is usually of the same size as, or rather larger than, the posterior (na_2), which was the opening of the olfactory organ and thus the real nasal aperture (Pl. 12, fig. 1; Pl. 15, figs. 2–6; Pl. 17, fig. 2; Pl. 18, figs. 2, 5; Pl. 19, figs. 1, 2; Pl. 20, fig. 3; Pl. 21; Pl. 22, figs. 5, 7; Pl. 23, figs. 1–3; Pl. 25, fig. 3; Pl. 26, fig. 2; Pl. 27, figs. 3, 4; Pl. 30, fig. 2; Pl. 35, figs. 1, 2; Pl. 47, fig. 2;

Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 51, figs. 1, 2; Pl. 52, fig. 1; Pl. 54, figs. 1–4; Pl. 55, figs. 1, 3; Pls. 61, 62) : but there are also individuals and even species in which the posterior division is bigger than the anterior (Pl. 1, figs. 2, 3; Pl. 4, fig. 2; Pl. 5, figs. 3, 5; Pl. 7, fig. 4). In *Thyestes*, *Didymaspis* and perhaps also *Sclerodus* [*Eukeraspis*], the naso-hypophysial aperture is rather long in proportion to the small size of the cephalic shield. The circum-nasal fossa is always well developed, but it is especially pronounced in *Thyestes* and *Didymaspis* (*f.cn*, text-figs. 23, 42, 60–62; Pl. 27, fig. 3; Pl. 40, fig. 2; Pl. 50, figs. 2, 3; Pl. 51, figs. 1, 2; Pl. 52, fig. 3; Pl. 54, figs. 1–4; Pl. 55, figs. 1, 3).

The ventral surface of the region shows, as in the Spitsbergen forms, the ethmoidal part of the aortic ridge (*r.aort*, Pl. 14, figs. 5–7; Pl. 25, fig. 1; Pl. 49, fig. 3; Pl. 53, fig. 5) and laterally to this a distinct paired sub-nasal fossa (*f.sn*, Pl. 53, fig. 5). In some specimens traces of the inter-branchial ridge 2 (Pl. 25, fig. 1) and the groove of the efferent branchial artery 2 (Pl. 25, fig. 1; $a.eff_2$, Pl. 49, fig. 3) are also to be seen on this surface.

The ethmoidal cavity, *i.e.* the cavity which lodged the olfactory organ and the anterior part of the hypophysial sac, is in the fossil condition in open communication with the cavum cerebrale cranii (Pl. 50, fig. 1) and seems also in all other respects to be as in the Spitsbergen forms. It is best preserved in *Sclerodus* [*Eukeraspis*], in which it is displayed both from the dorsal and ventral sides (Pl. 52, fig. 2; Pl. 53, fig. 5). In *Sclerodus*, *Thyestes*, *Didymaspis*, *Securiaspis* and *Benneviaspis* the ethmoidal cavity is lined by a perichondrial bone-layer, which forms a direct anterior continuation of the internal bone-layer, whereas in most of the other forms it seems to have been without such a lining, or provided with one so delicate that it could be preserved only in exceptional cases (*C. salweyi*).

The ethmoidal region is perforated by the canal of the n. profundus, as in the Spitsbergen forms, and this canal is fairly often well displayed. In *Sclerodus* it bends downwards and opens into the oralo-branchial chamber on the ventral side of the region, just in front of the sub-nasal fossa (V_1, Pl. 52, fig. 2), whereas in most other forms it continues forwards for some distance through the visceral endoskeleton in front of the region before it reaches the oralo-branchial chamber (V_1, text-figs. 9, 10, 12, 13; Pl. 4, fig. 4; Pl. 14, fig. 2; Pl. 18, fig. 6; Pl. 19, fig. 1; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, figs. 1, 3, 4; Pl. 51, fig. 2).

In *Hemicyclaspis*, *Cephalaspis*, except *C. powriei*, in *Securiaspis* and *Benneviaspis* the most postero-lateral part of this region is traversed by the common canal of the two most anterior nerves of the lateral electric field ($sel_{1,2}$, text-figs. 10, 12; Pl. 1, figs. 2, 3; Pl. 8, fig. 4; Pl. 15, fig. 1; Pl. 16, fig. 3; Pl. 18, figs. 5, 6; Pl. 19, fig. 2; Pl. 22, fig. 5; Pl. 23, fig. 2; Pl. 38, figs. 1, 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 3; Pl. 50, fig. 1), but in *C. powriei*, *Thyestes*, *Sclerodus* [*Eukeraspis*] and *Didymaspis* this canal does not enter the ethmoidal region, but curves ventro-laterally, passing down to the lateral electric field at some little distance postero-laterally to the orbit ($sel_{1,2}$, text-fig. 13; Pl. 26, fig. 1; Pl. 50, figs. 2–4; Pl. 51, figs. 1, 2, 5; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1). In species of *Hemicyclaspis* and *Cephalaspis*, except *C. powriei*, this canal bifurcates into its two main branches (*sel_1*, *sel_2*) at the antero-lateral corner of the orbit, and thus within the ethmoidal region; whereas in *Benneviaspis* and *Securiaspis* this bifurcation takes place further forward in the visceral endoskeleton. (For further details concerning the canal and its relations to other structures see the chapters on the visceral endoskeleton and the electric fields.)

The canal of the arteria facialis is preserved in several species (*a.fac*, text-figs. 9–12; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62), and, as previously mentioned, it is evident that its course and mode of branching are essentially as in the Spitsbergen forms. Among its branches the pre-mandibular and mandibular (*a.pm, a.am*, text-figs. 9–12; Pl. 20, fig. 3; Pl. 21; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62), the lateral infra-orbital (*a.iol*, text-figs. 9–12; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 2; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, fig. 1; Pl. 49, fig. 2; Pls. 61, 62), the medial infra-orbital (*a.iom*, text-figs. 9–12; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62), and the anterior (*a.fa*, text-figs. 10–12; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62) are not uncommonly preserved. These branches are especially well displayed in *Cephalaspis whitei* and the species of *Benneviaspis*.

The canal of the pre-orbital division of the v. capitis lateralis (*$v.cl_1$*) is shown in a good state of preservation, especially in *Cephalaspis whitei*, *Securiaspis kitchini*, the species of *Benneviaspis* and *Thyestes egertoni* (*$v.cl_1$*, text-figs. 9–13; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, fig. 3; Pl. 51, fig. 2; Pls. 61, 62). As in the Spitsbergen forms, it passes medially to the canal of the n. profundus, and opens into the orbit dorso-medially to this canal. The canals of the dorso-lateral superficial veins 1 and 2, which are the main branches carrying blood to it (*$v.ls_1$*, *$v.ls_2$*, text-figs. 9–13; Pl. 18, fig. 6; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, figs. 3, 4; Pl. 51, fig. 2; Pls. 61, 62), have, on the whole, a similar course and position to those in the Spitsbergen forms.

Cavum cerebrale cranii.—The cavum cerebrale cranii is imperfectly known, but it is evident that in all essential features it was as in the Spitsbergen forms (Pl. 8, fig. 4; Pl. 25, fig. 1; Pl. 50, fig. 1; Pl. 52, fig. 2; Pl. 53, fig. 5), and is in the fossil condition continuous with the ethmoidal cavity, which lodged the olfactory organ and the anterior part of the hypophysial sac. As noted above (pp. 10–13), it is lined by a well-developed perichondrial bone-layer—the internal perichondrial bone-layer—in *Sclerodus* [*Eukeraspis*], *Thyestes, Didymaspis* and *Securiaspis*, whereas in most other forms it has either a very delicate and imperfectly developed lining of perichondrial bone or else is entirely devoid of any such structure.

Dermal Cranial Roof.

As is obvious from the general account of the exo- and endo-skeleton of the cephalic shield (pp. 4–13), the exoskeleton which covers the dorsal surface of the endocranium, that is, the dermal cranial roof, is continuous with, and forms part of, the exoskeleton of the cephalic shield.

Visceral Endoskeleton.

In the visceral endoskeleton of the British species we may distinguish two divisions, as in the Spitsbergen forms: a dorsal division which is continuous with the endocranium and the endoskeletal shoulder-girdle and thus forms part of the cephalic shield; and a ventral division which formed part of the tissue that closed the oralobranchial fenestra. Concerning the position and mutual relations of these two divisions nothing new can be added here to what was said of them in the Spitsbergen monograph (Stensiö 1927, p. 144).

For details we first turn to the dorsal division. This division may, as in the Spitsbergen specimens, be considered to consist of an unpaired rostral part, a paired lateral part and an unpaired posterior part, the last constituting the post-branchial wall.

On the internal surface of the rostral part we find preserved in several specimens the area that formed, at least to a considerable extent, the roof of the mouth, and which has been termed above the supra-oral field (*dpr*). This area, which usually is more or less triangular in outline and somewhat concave both in transverse and longitudinal directions, is situated in many of the forms on a thickened portion of the rostral part of the visceral endoskeleton. It varies in size in different species; for instance, it is small in *Hemicyclaspis murchisoni*, *Cephalaspis whitei* and certain other species of *Cephalaspis* (Pl. 8, fig. 4; Pl. 14, fig. 7; Pl. 18, fig. 6; Pl. 20, fig. 3; Pl. 21; Pl. 28, figs. 1, 2; Pl. 37, fig. 1); whereas in *C. salweyi* (Pl. 25, fig. 1) and *Didymaspis grindrodi* (Pl. 54, fig. 2) it is moderately large. In *Didymaspis grindrodi* and *Hemicyclaspis murchisoni* it is equipped as in *Thyestes verrucosus*, *Micraspis gracilis* and *Tremataspis* (*cf.* Stensiö 1927, p. 150, and Kiaer 1928, pp. 127–129) with tooth-like tubercles (Pl. 8, fig. 4; Pl. 54, fig. 2), which in *H. murchisoni*, however, are confined to a fairly narrow median area. In the species of *Cephalaspis* in which the supra-oral field is known in detail, it is, on the contrary, devoid of such tubercles, or at least has none that are distinct, and it seems not unlikely that this was also the case in species of several other genera. From its position and relations to other structures it is beyond question that its bony covering, which is undoubtedly of exoskeletal origin, is homologous with the maxillary tooth-plate of the Pteraspids (*cf.* Kiaer 1928), and therefore I shall here adopt the term *maxillary tooth-plate* for it. It must, however, be understood that the maxillary tooth-plate as thus defined is not a real, discrete plate, as it forms an integral part of the visceral endoskeleton and certainly has nothing at all to do with the maxillary of fishes (*cf.* the chapter on the Pteraspids below). The maxillary tooth-plate in the British forms is, just as in the Spitsbergen forms, bounded posteriorly on each side by a distinct pre-branchial ridge (*r.pm*, Pl. 25, fig. 1; Pl. 54, fig. 2) which, as I have shown, is serially homologous with the inter-branchial ridges and represents the dorsal part of a pre-mandibular visceral arch (*cf.* Stensiö 1927, pp. 155–167, 180). The rostral part of the aortic ridge, which is always present on this surface of the rostral part of the visceral endoskeleton, runs forwards as a rule only to the posterior angle of the supra-oral field (*r.aort*, Pl. 14, fig. 7; Pl. 20, fig. 3; Pl. 21; Pl. 28, figs. 1, 2; Pl. 54, figs. 1, 2). In *C. salweyi*, however, it is clear that it ends rather further forwards on the supra-oral field itself (Pl. 25, fig. 1). Here in *C. salweyi* are no traces of an aortic groove, but this is only natural, for the aorta could not have reached so far forward, since it arose by the confluence of the efferent branchial arteries, all of which lay more to the rear.

The lateral part of the dorsal division of the visceral endoskeleton is perforated in *Sclerodus* by the two most anterior of the four big fenestrae which are found there along the lateral margin of the cephalic shield. On the external surface of this part we always find the lateral electric field, which, however, continues backwards to the shoulder-girdle part of the shield.

On the internal surface of the lateral part of the dorsal division of the visceral endoskeleton and on the adjacent surface of the corresponding half of the post-branchial wall, there are in all the British forms in which these parts could be studied, as in the Spitsbergen forms, more or less deep branchial fossae (k_1–k_{10}, Pl. 6, figs. 1–3; Pl. 7, fig. 5; Pl. 8, fig. 4; Pl. 11, fig. 1; Pl. 25, fig. 1; Pl. 52, figs. 3, 4; Pl. 54, figs. 1, 2; Pl. 55, fig. 2) which are separated ventrally by inter-branchial septa (ibs_1–ibs_{10}) and dorsally by low inter-branchial ridges (ibr_2–ibr_{10}) forming the dorsal continuations of the inter-branchial septa. The total number of these fossae seems to be ten, at least in all the more typical British forms, and as this is also the case in the Spitsbergen forms, it seems very likely that this number is constant in the Cephalaspids. As the branchial fossae, the inter-branchial ridges, and inter-branchial septa of the British forms are known only as more or less imperfect impressions, nothing can be learned of their details, but it is probable that these were, in all essentials, as in the Spitsbergen forms.

Among the nerve canals which perforate the dorsal division of the visceral endoskeleton, those which transmitted the n. profundus (V_1), the n. trigeminus proper (V_2), the n. facialis (*VII*) and the n. glossopharyngeus (*IX*) to the oralo-branchial chamber are preserved in a few cases only (V_1, V_2, *VII*, *IXa*); but the canals of the nerves of the lateral electric field ($sel_{1,2}$, sel_1, sel_2–sel_6) are not uncommonly present, and, in fact, they are the most usually preserved of all the canals of this division of the visceral endoskeleton.

The canal of the n. profundus (V_1) as a rule runs forwards from the ethmoidal region for a fair distance through the rostral part of the dorsal division of the visceral endoskeleton before it turns downwards and opens into the oralo-branchial chamber (text-figs. 9, 10, 12, 13; Pl. 4, fig. 4; Pl. 14, fig. 2; Pl. 18, fig. 6; Pl. 19, fig. 1; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, figs. 1, 3, 4; Pl. 51, fig. 2). In *Sclerodus* [*Eukeraspis*] *pustuliferus*, however, it does not enter the rostral part, but, as pointed out in the description of the ethmoidal region, it curves downwards and opens into the oralo-branchial chamber while still within the ethmoidal region (V_1, Pl. 52, fig. 2). The arrangement is such, however, that the n. profundus after its entrance in the oralo-branchial chamber must have passed downwards behind the pre-branchial ridge in the normal way.

The canal of the n. trigeminus proper (V_2, text-figs. 10, 12, 13; Pl. 25, fig. 2;

Pl. 48, figs. 1, 2; Pl. 49, fig. 1; Pl. 50, figs. 1, 3, 4; Pl. 51, fig. 2; Pl. 52, fig. 2), the canal of the n. facialis (*VII*, text-figs. 10, 13; Pl. 48, fig. 2; Pl. 49, fig. 1; Pl. 51, fig. 2; Pl. 52, fig. 2; Pl. 53, fig. 5) and the canal of the n. glossopharyngeus (*IXa*, Pl. 25, fig. 1) usually traverse the upper middle region of this division of the visceral endoskeleton for a considerable distance before they reach and open into the oralo-branchial chamber.

All the canals of the lateral electric field pierce that part of the visceral endoskeleton situated dorso-medially to the lateral electric field. Since the two most anterior of these canals are always united with each other in a common canal for some distance (see p. 31), we may distinguish in the visceral endoskeleton between the common canal and the independent canals.

In the genera *Hemicyclaspis*, *Cephalaspis*, except *C. powriei*, *Benneviaspis* and *Securiaspis* the common canal ($sel_{1,2}$) has a course fairly similar to that in the Spitsbergen forms, *i.e.* it runs close to the side of the orbit and does not curve towards the lateral electric field until at the antero-lateral corner of the orbit. In *Hemicyclaspis* and *Cephalaspis* (*C. powriei* excepted) it reaches forwards only as far as the antero-lateral corner of the orbit before breaking up into the two canals ($sel_{1,2}$, sel_1, sel_2, Pl. 1, figs. 2, 3; Pl. 4, fig. 4; Pl. 5, fig. 2; Pl. 8, fig. 4; Pl. 14, figs. 2, 7; Pl. 15, figs. 1, 5; Pl. 17, fig. 2; Pl. 18, figs. 2, 5, 6; etc.), and thus does not enter the dorsal division of the visceral endoskeleton as a single unit. Of the two canals, which are in this case fairly long, one (sel_1) runs anteriorly, and the other (sel_2) posteriorly to the canal of the n. trigeminus proper (V_2). In *Benneviaspis* and *Securiaspis* the common canal continues a little further, to a point about midway between the antero-lateral corner of the orbit and the lateral electric field ($sel_{1,2}$, sel_1, sel_2, text-figs. 10, 12; Pl. 47, fig. 1; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pl. 50, fig. 1), and thus enters the visceral endoskeleton; consequently the independent canals are fairly short, and they, as well as the most anterior part of the common canal, are usually situated in front of the canal of the n. trigeminus proper (V_2).[1]

In *Sclerodus* [*Eukeraspis*], *Thyestes*, *Didymaspis* and *Cephalaspis powriei* the common canal takes a course somewhat different from that in the other forms just dealt with; for it passes not only more latero-ventrally to the orbit, but also curves towards the lateral electric field much further to the rear. In *Sclerodus* [*Eukeraspis*], *Thyestes* and *Didymaspis* it curves towards the lateral electric field far back, just posteriorly to the canal which transmitted the n. facialis from the labyrinth cavity to the oralo-branchial chamber (*VII*), and, moreover, continues without bifurcation down to, or almost down to, the lateral electric field, so that two independent canals are not to be found. During its course in the visceral endoskeleton in these three genera the common canal always retains its position close behind the canal which transmitted the n. facialis (*VII*) to the oralo-branchial chamber ($sel_{1,2}$, text-fig. 13; Pl. 50, figs. 2–4; Pl. 51, figs. 1, 2; Pl. 52, fig. 2; Pl. 54, fig. 4;

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[1] In the specimen of *Securiaspis kitchini* shown in Pl. 49, fig. 1, the two most anterior of the canals of the nerves of the lateral electric field of the left side are independent of one another from near the antero-lateral corner of the orbit, and run on either side of the canal of the n. trigeminus proper. Their development in this specimen is thus exactly as in *Hemicyclaspis* and the majority of the species of *Cephalaspis* on the left side, and as in *Benneviaspis* and the other species of *Securiaspis* on the right.

Pl. 55, fig. 1). In *Cephalaspis powriei* it does not turn off towards the lateral electric field quite as far back as in these genera, but at a point between the canals of the n. trigeminus proper (V_2) and the canal (VII) through which the n. facialis reached the oralo-branchial chamber. Shortly afterwards it passes into the independent canals (sel_1 and sel_2), which are thus fairly long in this species, almost as long as in the other species of *Cephalaspis* ($sel_{1,2}$, sel_1, sel_2, Pl. 26, fig. 1; Pl. 28, fig. 2). In *C. powriei* the first of these independent canals (sel_1) crosses the canal of the n. trigeminus proper (V_2) and goes down to the lateral electric field in front of that canal, whereas the second remains in its original position posterior to the canal of the n. trigeminus proper (V_2) during the whole of its course to the lateral electric field; they thus have similar relations to the canal of the n. trigeminus proper (V_2) in *C. powriei* as in the other species of *Cephalaspis*, and it is therefore evident that, despite the somewhat different course of their common part, they agree on the whole with those in *Hemicyclaspis* and *Cephalaspis*. Thus the two most anterior nerves of the lateral electric field in *Thyestes*, *Didymaspis* and *Sclerodus* [*Eukeraspis*] passed down to their field much further backwards than in all the other Cephalaspids, and the reason for this lies in the development of the lateral electric field, which does not reach as far forward as in the other genera, so that its most anterior nerves, in order to reach their destination, had to turn further round and take a course much more posterior to the orbit and to the branchial nerves than in the other genera.

The canals of the four posterior nerves of the lateral electric field (sel_3–sel_6, text-figs. 9, 10, 12, 13; Pl. 4, fig. 4; Pl. 5, fig. 2; Pl. 14, figs. 1, 7; Pl. 15, figs. 1, 5; Pl. 16, figs. 3, 4; Pl. 18, figs. 5, 6; Pl. 19, figs. 1, 2, 3; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 23, figs. 2, 3; Pl. 25, fig. 1; Pl. 26, fig. 1; Pl. 28, fig. 2; Pl. 30, fig. 2; Pl. 35, figs. 1, 2; Pl. 38, figs. 1, 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pl. 50, figs. 1–4; Pl. 51, fig. 2; Pl. 52, fig. 2; Pl. 54, fig. 4; Pl. 55, fig. 1; Pls. 61, 62) are always independent of each other throughout their length, and their course is similar in all the Cephalaspids.

We have already seen that there is a distinct aortic ridge on the internal surface of the rostral part of the dorsal division of the visceral endoskeleton (*r.aort*, Pl. 14, fig. 7; Pl. 20, fig. 3; Pl. 21; Pl. 25, fig. 1), and in some species this ridge is provided with a somewhat pronounced aortic groove (*aort.gr*, Pl. 28, fig. 1). In addition, in a few instances there are traces on this same surface of the grooves of the rostral artery (*a.rostr*, Pl. 25, fig. 1; Pl. 28, figs. 1, 2) and of the efferent branchial artery 1 ($a.eff_1$, Pl. 25, fig. 1; Pl. 49, fig. 3). The arterial canals which are preserved in the dorsal division are those of the a. facialis and its branches (*a.fac, a.fa, a.pm, a.am, a.iol, a.iom*, text-figs. 9–12; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, fig. 2; Pls. 61, 62), the dorso-lateral superficial arteries (*a.sa*, $a.sm_1$, $a.sm_2$, *a.sp*, text-figs. 9–12; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pls. 61, 62) and—in a single specimen of *Benneviaspis anglica*—a part of the canal of the a. sub-clavia.

The venous canals of the dorsal division are usually better preserved than those of the arteries. Remains are to be found of the canals of the rostral vein sinus (*vs.r*, Pl. 25, fig. 1), the rostral veins (*vv.rs*, text-figs. 10–12; Pl. 47, fig. 2; Pl. 48, figs. 1, 2), the marginal vein (*v.marg*, Pl. 50, fig. 4) and the dorso-lateral superficial veins (*v.ls*$_1$–*v.ls*$_6$, text-figs. 9–13; Pl. 18, fig. 6; Pl. 19, fig. 2; Pl. 20, fig. 3; Pl. 21; Pl. 22, fig. 5; Pl. 25, fig. 2; Pl. 26, fig. 1; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs 1, 2; Pl. 50, fig. 3; Pl. 51, fig. 2; Pls. 61, 62), all of which are in the main as in the Spitsbergen forms. In *Benneviaspis anglica* and *B. lankesteri*, however, it is clear that the distal parts of the canals of the dorso-lateral superficial veins may be somewhat widened in places, giving rise to small superficial sinuses (text-figs. 10–12; Pl. 47, fig. 2; Pl. 48, figs. 1, 2). In addition, in both these species between the distal parts of the canals of the dorso-lateral superficial veins there are certain other vein canals which pass down to the lateral electric field and are not infrequently wider than the canals of the dorso-lateral superficial veins (*v.dls*, text-figs. 10, 11; Pl. 47, fig. 2; Pl. 48, fig. 2). While the dorso-lateral superficial veins carried blood from the lateral electric field dorso-medially to the v. capitis lateralis, the veins lodged in the canals leading to the lateral electric field evidently brought blood to that field. Since, however, they seem to have been often wider than the dorso-lateral superficial veins, the latter cannot alone have sufficed for draining the lateral electric field, but this field must have been drained in addition by veins which emptied into the marginal vein.

Of the ventral division of the visceral endoskeleton no remains have been discovered hitherto, and it seems, therefore, that this was entirely cartilaginous. Under such circumstances, of course, very little can be learned concerning it. From the development of its exoskeleton it is probable, however, that it was very flexible in order to facilitate the functions of feeding and respiration, for it must have played an important part in both of these. Very possibly it consisted either of a single plate of cartilage or of a number of such plates, but in any case it is not likely that it was developed as a series of typical, independent visceral arches.

Visceral Exoskeleton.

In the visceral exoskeleton we may, as in the visceral endoskeleton, distinguish a dorsal and a ventral division.

The dorsal division is a continuous mass of dermal bone which forms part of the exoskeletal component of the cephalic shield. It reaches downwards to the external branchial openings, forming their lateral boundary. Dorsally it is continuous with the dermal cranial roof, and posteriorly with the exoskeletal shoulder-girdle. In *Sclerodus* this division is perforated by the two most anterior of the four big fenestrae which occur along the margin of each side of the cephalic shield (*for*$_1$–*for*$_4$, text-fig. 62; Pl. 52, figs. 1, 2; Pl. 53, fig. 5).

The ventral division, or—as it is termed here—the ventral visceral exoskeleton, is, like the corresponding division of the visceral endoskeleton, independent of the cephalic shield, and consists of separate, but often closely appressed, polygonal plates. Among the British forms it is best known in *Hemicyclaspis murchisoni*, but remains of it are also to be seen in *Cephalaspis pagei* and *Thyestes egertoni* (*vv.es*, Pl. 51, fig. 4), while in the Norwegian forms it is preserved both in *Micraspis gracilis* and *Aceraspis robusta* (Kiaer 1928).

In *Hemicyclaspis murchisoni* (text-fig. 8; Pl. 6, figs. 1–3; Pl. 7, fig. 3) the plates of the ventral visceral exoskeleton are small and very numerous; and the most posterior of them vary rather, both in number and shape, in different specimens. Thus in the specimen figured in Pl. 6, fig. 1, they are small in the postero-median area, whereas on each side and in front of this area they are somewhat larger; but in the specimens figured in Pl. 6, fig. 3 and Pl. 7, fig. 3, in the corresponding area they almost equal in size the other plates nearest them. Along each lateral border of the oralo-branchial fenestra, especially along the posterior half, some fairly large plates are to be found in all the specimens. The most antero-median plates preserved are easily distinguished from all the others by their much smaller size, by their rhombic shape and by their arrangement in distinct rows.

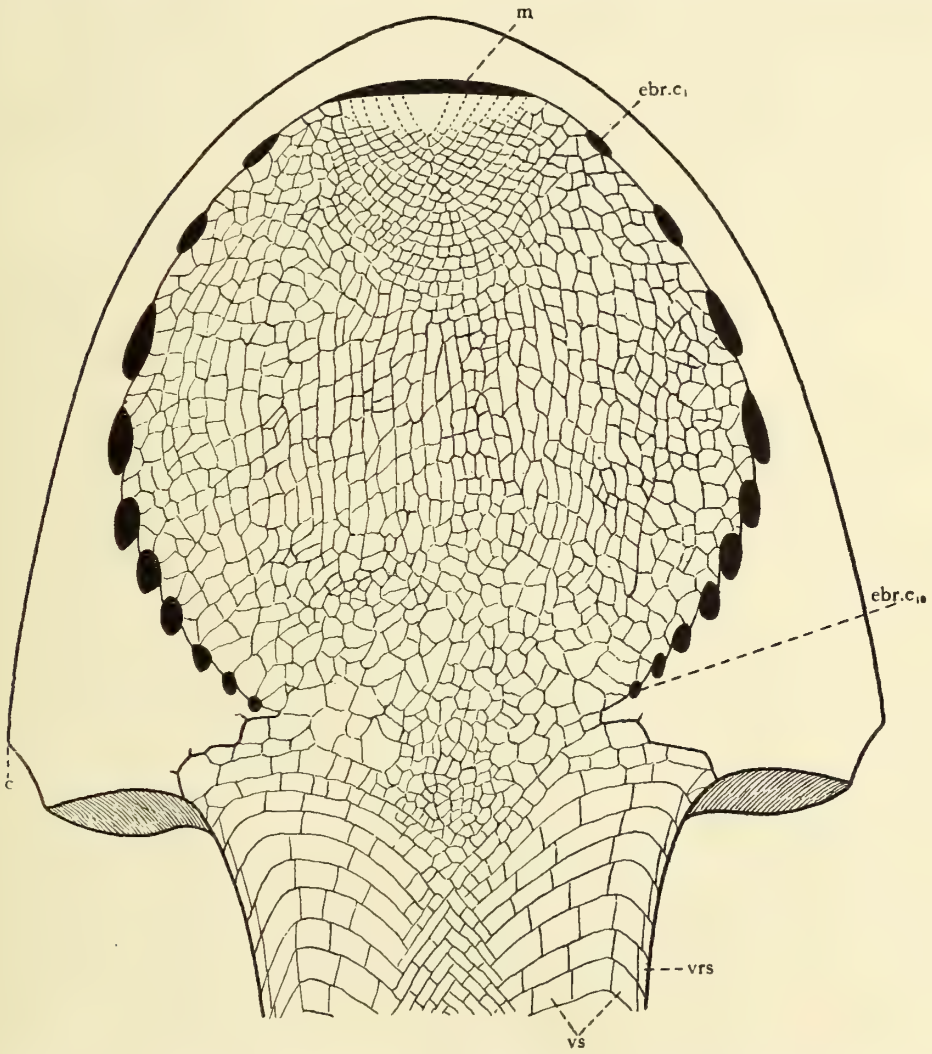
Both in *Cephalaspis pagei* and *Thyestes egertoni* the plates of the ventral visceral exoskeleton are in the main, and as far as they are known, just as described in *Hemicyclaspis murchisoni.*

In *Micraspis gracilis* (text-fig. 2) the ventral visceral exoskeleton is even more completely known than in *Hemicyclaspis murchisoni,* and it is arranged in essentially the same way. Thus the posterior and postero-lateral plates are larger than the others, but they are much larger relatively than in *H. murchisoni* and accordingly fewer in number. Moreover, the antero-median plates are small, rhombic in shape and arranged in the same way as in *H. murchisoni.* Finally, in *Micraspis* there follows immediately behind the mouth-opening a series of eleven fairly large plates, which from their relation to the mouth-opening were termed *oral plates* by KIAER. Of such plates nothing has been found in *Hemicyclaspis murchisoni.* The median plate of these eleven in *Micraspis* seems to be somewhat triangular in shape, whereas the five on each side of it are generally four-sided and longer than broad.

In *Aceraspis robusta* the ventral visceral exoskeleton consists, at least to a large extent, of very small plates which are suggestive of *Thelodus*-scales (KIAER 1928).

Since the ventral visceral exoskeleton of *Hemicyclaspis murchisoni* does not differ, as far as it is preserved, in any essential point from that in *Micraspis gracilis*, it follows that it was also equipped anteriorly with a series of oral plates; and since it is possible that the ventral visceral exoskeleton was developed in this way in *Cephalaspis pagei* and *Thyestes egertoni* also, we are forced to the conclusion that it was thus developed in the Cephalaspids in general. Thus we find in the Cephalaspids not only a maxillary tooth-plate but also distinct oral plates agreeing with those of the Pteraspids, and it is therefore obvious that the mouth in the Cephalaspids was of the same peculiar type as in the Pteraspids (*cf.* KIAER 1928). This fact is of great interest as it shows that this type of mouth must be very old, and there is even reason to assume that it had already arisen in the primitive ancestors of both the *Osteostraci* and *Heterostraci.* In this connection it should be noted that the subdivision of the ventral visceral exoskeleton into a great number of small plates clearly indicates that the entire mass of tissue that filled the oralo-branchial fenestra, and thus formed the ventral wall of the oralo-branchial chamber, was very flexible, and that it underwent considerable movement during the processes of feeding and respiration. On this account it seems impossible that the ventral division of the visceral endoskeleton could have consisted of rigid visceral arches; it must have been represented either by a continuous, very flexible mass of cartilage, or else by a number of independent flexible cartilaginous plates.

How the plates of the ventral visceral exoskeleton were situated in relation to the external branchial openings cannot be definitely established. It seems most likely, however, that they did not cover these openings, but that the arrangement was very much as in *Tremataspis* (text-fig. 8).



TEXT-FIG. 8.—*Hemicyclaspis murchisoni* (EGERTON). Attempted restoration of the ventral visceral exoskeleton. Approx. × 2 diam.
c, angle representing the cornu; *ebr.c*$_1$, *ebr.c*$_{10}$, external branchial openings; *m*, mouth-opening; *vrs*, ventro-lateral scales; *vs*, ventral scales.

The plates of the ventral visceral exoskeleton are composed of three layers, corresponding to those of the exoskeleton of the cephalic shield. The superficial layer and the superficial parts of the middle layer form a continuous covering on each plate in those forms, or in those individuals, in which they are continuous on the exoskeletal component of the cephalic shield and on the scales; whereas they are subdivided into isolated tubercles when thus represented elsewhere on the exoskeleton. As in all the plates there are distinct remains of ascending vascular canals (*c.asc*, Pl. 6, figs. 1–3; Pl. 7, fig. 3), it is probable that each plate corresponds according to its size to one or more polygonal areas (*cf.* pp. 24–25). The mucous canal system of the plates could not be studied, but everything seems to indicate that it was present and developed as in the cephalic shield. Where the plates are very small it probably lay, at least to a great extent, in the soft tissues between the plates; where they are larger the intra-areal canals lay either in, or more or less superficially to, them; but where the plates are very large not only the intra-areal but probably also some of the inter-areal canals were either enclosed in, or situated superficially to, them.

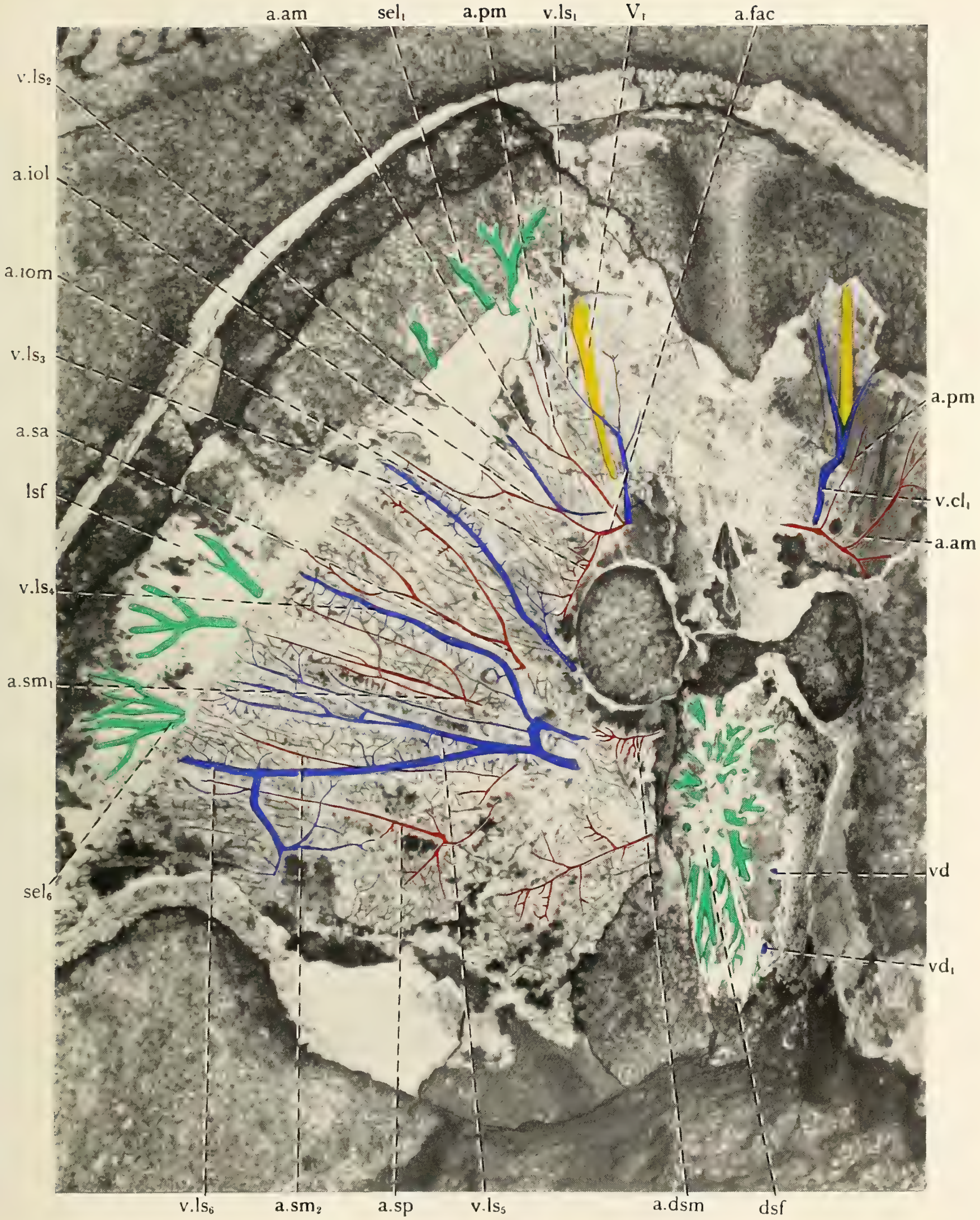
Cranial Nerves.

The cranial nerves in the British Cephalaspids were in all essentials as in the species from Spitsbergen, and thus it is not necessary to describe them in detail here, but the reader is referred to the monograph on the Spitsbergen Cephalaspids (Stensiö 1927, pp. 189–204). A few remarks, however, on the two most anterior nerves of the lateral electric fields are necessary, since these nerves, both in their mutual relations and relations to other nerves, were much less constant than the other cranial nerves.

The two anterior nerves of the lateral electric fields were developed in a similar way in all the forms, inasmuch as they were always united in a common trunk which ran from the bottom of the labyrinth cavity for a considerable distance forwards. In certain forms this common trunk ended at its entrance into the dorsal division of the visceral endoskeleton; in others it continued for some distance into that division; while in still others it continued down to the lateral electric field itself. Thus the independent portions of the nerves were of very different lengths in the various forms, some not being developed until the lateral electric field was reached. Both the common trunk and the independent parts of the nerves varied somewhat in their relation to the orbit and the trigeminus proper in the different forms, and on this point the British Cephalaspids may be subdivided into four groups.

To the first of these groups *Hemicyclaspis* and *Cephalaspis*, with the exception of *C. powriei*, are to be referred. In this group the common trunk of the nerves in question passed forwards close to the side of the orbit, and crossed during this passage the n. trigeminus proper on the dorsal side. It reached, however, only to the antero-lateral corner of the orbit, where its two components separated from each other and turned down obliquely towards the lateral electric field. The two nerves were thus independent of each other after reaching the antero-lateral corner of the orbit. During their course thence to their entrance into the electric field, the anterior passed in front of, and the posterior behind, the n. trigeminus proper.

The second group is represented by *Cephalaspis powriei* alone. In this the common trunk of the two nerves was a little longer than in the other species of *Cephalaspis*,



TEXT-FIG. 9.—*Cephalaspis whitei*, sp. nov. System of superficial vessels on the dorsal side of the endoskeleton of the cephalic shield. The electric nerves, green; the ordinary cranial nerves, yellow; arteries, red; and veins, blue. Chiefly after specimen no. P. 5048 in the British Museum (Pl. 20, fig. 3; Pl. 21). > × 3 diam.

a.am, mandibular branch of the a. facialis; *a.dsm*. arteria superficialis post-orbitalis; *a.fac*, arteria facialis; *a.pm*, pre-mandibular branch of the a. facialis; *a.iol*, lateral infra-orbital branch of the a. facialis; *a.iom*, medial infra-orbital branch of the a. facialis; *a.sa*, *a.sm*$_1$, *a.sm*$_2$, *a.sp*, dorso-lateral superficial arteries 1–4; *dsf*, dorsal electric field; *lsf*, lateral electric field; *sel*$_1$–*sel*$_6$, nerves of the lateral electric field; *v.cl*$_1$, pre-orbital division of the v. capitis lateralis; *vd*, *vd*$_1$, veins from the dorsal electric field; *v.ls*$_1$–*v.ls*$_6$, dorso-lateral superficial veins 1–6; *V*$_1$, n. profundus.

and in addition did not pass close to the orbit, but turned ventro-laterally towards the lateral electric field a short distance behind it; thus it did not cross the n. trigeminus proper as in the other species of *Cephalaspis*, but lay entirely posterior to it. After separating from each other, the two nerves continued down to the lateral electric field in such a way that the anterior crossed the n. trigeminus proper and continued in front of it, whereas the second remained posterior to it, their courses being similar to those in the other species of *Cephalaspis*. This group is thus characterized by the following relations of the two most anterior nerves of the lateral electric field: their common trunk ran a short distance into the dorsal division of the visceral endoskeleton, but its course was such that the n. trigeminus proper passed downwards to the oralo-branchial chamber in front of it, whereas their independent parts were placed as in *Hemicyclaspis* and the other species of *Cephalaspis*, *i.e.* so that the n. trigeminus proper passed in the space between them.

The third group comprises the genera *Benneviaspis* and *Securiaspis*. In this group the common trunk of the two anterior nerves passed forward close to the orbit and crossed the n. trigeminus proper, as in *Hemicyclaspis* and the majority of the species of *Cephalaspis*, but did not separate into its components at the antero-lateral corner of the orbit; instead, it continued antero-laterally to a point about midway between this corner and the lateral electric field. Accordingly, here it reached forwards into the dorsal division of the visceral endoskeleton antero-ventro-laterally to the orbit, and owing to this the independent parts of the nerves were fairly short. The independent parts of the nerves, as well as the anterior part of their common trunk, all situated in the dorsal division of the visceral endoskeleton, ran as a rule in front of the n. trigeminus proper. Besides *Benneviaspis* and *Securiaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis* also are referable to this group. In *Boreaspis* and *Kiaeraspis* the two nerves were, however, united in a common trunk until their entrance into the lateral electric field, and in this they agree with those forms belonging to the fourth and last group.

Finally, the fourth group includes the genera *Thyestes*, *Didymaspis* and *Sclerodus* [*Eukeraspis*]. In this group, as in the genera *Boreaspis* and *Kiaeraspis*, the common trunk of the two nerves continued down to the lateral electric field, thus perforating completely that part of the dorsal division of the visceral endoskeleton situated dorsally to the lateral electric field. In addition, the common trunk never reached the orbit but turned down obliquely towards the lateral electric field at some distance behind it. On this account it lay so far posteriorly in the dorsal division of the visceral endoskeleton that it ran posteriorly not only to the n. trigeminus proper but also to the n. facialis.

CRANIAL VESSELS.

The cranial vessels of the British Cephalaspids were in all essentials developed as in the Spitsbergen Cephalaspids (*cf.* STENSIÖ 1927, pp. 204–231), even in some of the finest details (text-figs. 9–13), and it is therefore unnecessary to give a further account of them here. From this we may draw the important conclusion that the vascular system of the Cephalaspids in general was constant both in regard to its position and its mode of branching.

In this connection we may note that in *Benneviaspis lankesteri* (text-fig. 11) and *Benneviaspis anglica* (text-fig. 10) the posterior dorso-lateral superficial veins were so widened in places somewhat dorso-medial to the lateral electric field that vein-sinuses were formed; also in these two species there were short but rather wide veins between the distal parts of the dorso-lateral superficial veins which carried blood down to the lateral electric field (*v.dls*). Since the dorso-lateral superficial veins were, as a rule, narrow where they left the lateral electric field, it is evident that they cannot have drained this field completely, but that a considerable quantity of the venous blood from it must have been brought down to the marginal vein by means of short veins passing ventro-laterally.

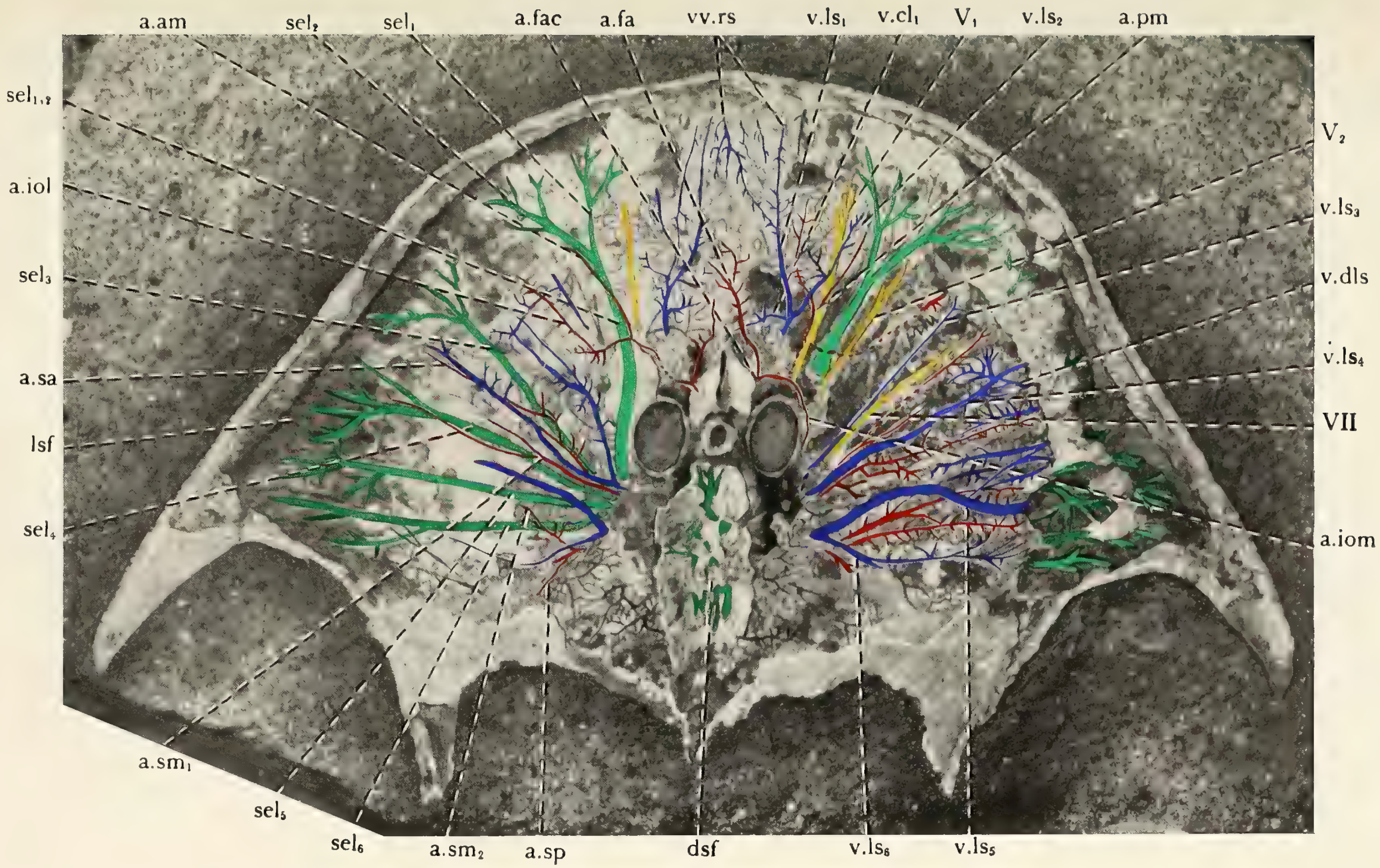
Finally, it should be pointed out that both the sub-aponeurotic (sub-cutaneous) vascular plexus (Pl. 20, fig. 3; Pl. 21; Pl. 47, fig. 2; Pl. 48, figs. 1, 2; Pl. 49, figs. 1, 2; Pls. 61, 62: *dplx*, text-fig. 6; Pl. 64, figs. 2, 3) and the sub-epidermal vascular plexus (text-figs. 6, 7; Pl. 41, figs. 1, 2; Pl. 44, figs. 1–3; Pl. 57, fig. 2; Pl. 58, figs. 2, 3; Pl. 59, figs. 3–5; Pl. 60, figs. 1–4; Pl. 63, figs. 1–3; Pl. 64, figs. 1–3) are very well developed and that the moderately wide pores, which perforate the superficial layer when that is continuous throughout its extent, are not vascular canals at all, as was maintained by the present writer in the description of the Spitsbergen forms (see Stensiö 1927, p. 36), but simply openings of the mucous canal system, which in such cases is enclosed in the exoskeleton (*cf.* pp. 13, 19).

The Electric Fields.

The electric fields are usually well preserved in the British forms, in all of which they consist, as in the Spitsbergen Cephalaspids, of an unpaired dorsal field and a pair of lateral fields, the latter always being continuous throughout their extent and not divided into two, as in *Tremataspis* (*cf.* Stensiö 1927, p. 308).

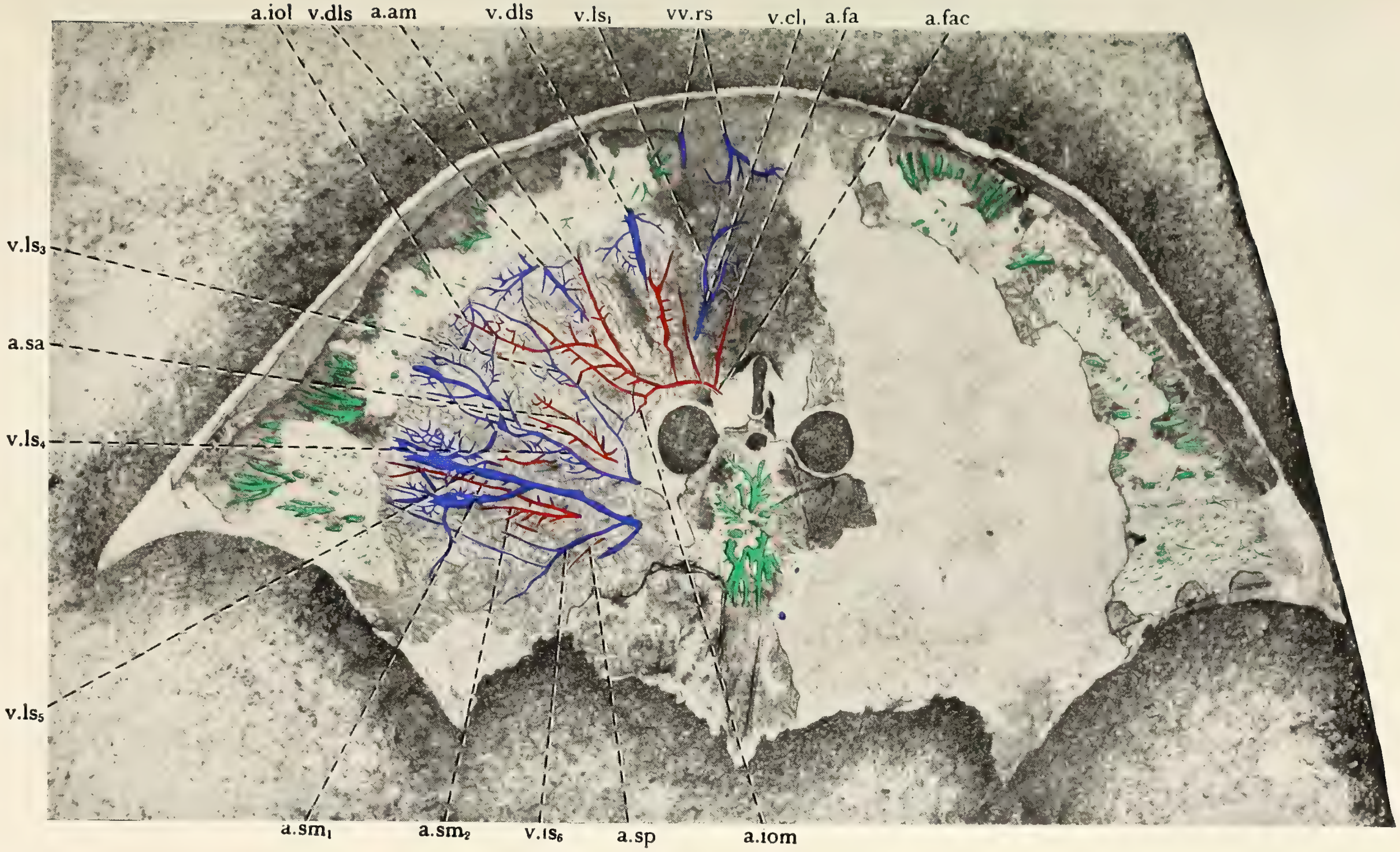
The dorsal electric field is best developed in *Hemicyclaspis, Cephalaspis, Benneviaspis* and *Securiaspis* (*dsf*, text-figs. 1A, C, 9–13, 23, 27, 29, 30, 33–37, 39–48, 50, 55–58; Pls. 1–5, 7, 12–23, 25–31, 35–40, 43, 46–49, 62), in which its anterior end usually lies immediately behind the pineal depression, and its posterior, rather far back on the occipital region. It is very characteristic of the dorsal field in these genera that it always reaches so far back that the external orifice of the paired canal (d_1), which perhaps lodged the ductus endolymphaticus, opens into it at some distance anterior to its hinder end. In *Didymaspis, Thyestes* and *Sclerodus* [*Eukeraspis*], in which it is shorter than in the genera just mentioned, it begins some way behind the pineal depression (*dsf*, text-figs. 59–62; Pls. 50–55), especially in *Sclerodus*, and reaches only so far back as to enable the paired canal (d_1) to open into it just at its postero-lateral corners, or perhaps in certain species even immediately behind these.

Like the dorsal electric field, the lateral fields are longest and best developed in *Hemicyclaspis, Cephalaspis, Benneviaspis* and *Securiaspis* (*lsf*, text-figs. 9–12, 15, 23, 25, 27–39, 41–46, 48–50, 52–58; Pls. 1–8, 11–32, 35–40, 43, 46–49). In all these genera they are always fairly broad and extend backwards from a point situated far forward on the dorsal division of the visceral skeleton on to the cornua, or—as in



TEXT-FIG. 10.—*Benneviaspis anglica*, sp. nov. System of superficial vessels on the dorsal side of the endoskeleton of the cephalic shield. The electric nerves, green; the ordinary cranial nerves, yellow; arteries, red; and veins, blue. Chiefly after specimen no. 46568 in the British Museum (Pl. 48, fig. 2). × 3 diam.

a.am, pre-mandibular branch of the a. facialis; *a.fa*, anterior branch from the a. facialis; *a.fac*, arteria facialis; *a.iol*, lateral infra-orbital branch of the a. facialis; *a.iom*, medial infra-orbital branch of the a. facialis; *a.pm*, pre-mandibular branch of the a. facialis; *a.sa*, $a.sm_1$, $a.sm_2$, *a.sp*, dorso-lateral superficial arteries 1–4; *dsf*, dorsal electric field; *lsf*, lateral electric field; $sel_{1,2}$, common trunk of the two most anterior nerves of the lateral electric field; sel_1–sel_6, nerves of the lateral electric field; $v.cl_1$, pre-orbital division of the v. capitis lateralis; *v.dls*, vein sinuses leading down to the lateral electric field; $v.ls_1$–$v.ls_6$, dorso-lateral superficial veins 1–6; *vv.rs*, rostral veins; V_1, n. profundus; V_2, n. trigeminus proper; *VII*, n. facialis.



TEXT-FIG. 11.—*Benneviaspis lankesteri*, sp. nov. System of superficial vessels of the dorsal side of the endoskeleton of the cephalic shield. The electric nerves, green; the arteries, red; the veins, blue. Chiefly after specimen no. 46877 in the British Museum (Pl. 47, fig. 2). × 3 diam.

a.am, pre-mandibular branch of the a. facialis; *a.fa*, anterior branch from the a. facialis; *a.fac*, arteria facialis; *a.iol*, lateral infra-orbital branch of the a. facialis; *a.iom*, medial infra-orbital branch of the a. facialis; *a.sa*, $a.sm_1$, $a.sm_2$, *a.sp*, dorso-lateral superficial arteries 1–4; $v.cl_1$, pre-orbital division of the v. capitis lateralis; *v.dls*, vein sinuses leading down to the lateral electric field; $v.ls_1$, $v.ls_3$–$v.ls_6$, dorso-lateral superficial veins 1, 3–6; *vv.rs*, rostral veins.

Hemicyclaspis in which cornua are lacking—almost to the very posterior margin of the zonal part in front of the pectoral sinuses. On account of their extent so far forward in these genera they are crossed obliquely in their rostral part by the infra-orbital sensory canal groove. In *Didymaspis* (*lsf*, text-fig. 61; Pl. 54, fig. 3; Pl. 55, figs. 3, 4), *Sclerodus* [*Eukeraspis*] (*lsf*, text-fig. 62; Pl. 52, figs. 1, 2) and to a certain extent also in *Thyestes* (*lsf*, text-fig. 60; Pl. 27, figs. 3, 4; Pl. 50, fig. 2) they do not reach so far forward as in the genera just mentioned, in *Didymaspis* their anterior end lying far behind the infra-orbital sensory canal groove; moreover, in these three genera they never extend on to the cornua, even if these, as in *Sclerodus*, attain a very considerable size. In *Didymaspis* the lateral fields are strikingly narrow; in *Sclerodus*, on the contrary, fairly broad. In *Sclerodus* they are situated on the inner side of the four fenestrae which in that genus perforate the most ventro-lateral part of the dorsal division of the visceral skeleton and the adjacent portion of the zonal part (text-fig. 62; Pl. 52, figs. 1, 2; Pl. 53, figs. 5); but they are nothing whatever to do with these fenestrae. In *Benneviaspis*, *Thyestes* and *Didymaspis* the lateral electric fields are provided with a postero-medial angle which extends in a more or less oblique medial direction on to the zonal part of the cephalic shield. In *Benneviaspis* and *Thyestes* this angle is, as in *Hoelaspis*, fairly small and invades the zonal part but slightly, whereas in *Didymaspis*, as in *Boreaspis* and *Kiaeraspis*, it is strongly developed and so long that it extends right across that part. In *Hemicyclaspis*, *Cephalaspis*, *Securiaspis* and *Sclerodus* this angle is either absent or not distinctly developed.

The plates covering the electric fields are frequently preserved (text-figs. 1, 15, 23, 25, 33A; Pls. 1–7; Pl. 17, fig. 2; Pl. 25, fig. 3; Pl. 28, fig. 3; Pl. 30, figs. 1, 3; Pl. 31; Pl. 36, figs. 3, 4; Pl. 37, fig. 3; Pl. 38, figs. 3, 4; Pl. 39, figs. 1, 2; Pl. 40, fig. 1; Pl. 43). They are always present in great numbers and are situated close to each other, so close that the boundaries between them are sometimes hardly discernible (Pl. 5, fig. 6). Both their number and shape seem to vary, not only in different species, but also in different specimens of the same species. As pointed out in the description of the micro-structure of the exoskeleton of the cephalic shield (pp. 26–27), they are as thick as the exoskeleton of the cephalic shield, and consist of the same three layers (Pl. 5, fig. 6): thus the electric fields were situated either in the most basal part of the corium or immediately below it. As was also mentioned above, the micro-structure of the plates in question suggests that each of them is equivalent to a polygonal area of the exoskeleton of the cephalic shield itself.

The nerve canals and vascular canals of the electric fields have been dealt with in detail already and it is therefore superfluous to give any account of them here (*cf.* pp. 31–33, 35–36, 39–40, 44–45).

Shoulder-Girdle.

In the monograph of the Spitsbergen forms it was shown that the zonal part of the cephalic shield is probably the homologue of the shoulder-girdle of fishes and higher vertebrates (Stensiö 1927, pp. 231–235), and therefore this part of the cephalic shield will here be termed the shoulder-girdle.

The general shape and relations of the shoulder-girdle of the British forms have already been dealt with to some extent in the general account of the cephalic shield (*cf.* pp. 9–10), and from that description it was clear that in all features of any importance the girdle is like that of the Spitsbergen forms. As in the endoskeleton of the cephalic shield, its endoskeleton was cartilaginous and lined by a perichondrial bone-layer, which is continuous with, and forms part of, the external perichondrial bone-layer (*cf.* pp. 10–13). This perichondrial bone-layer, however, seems in the majority of the species of *Cephalaspis* to have been very delicate or perhaps even entirely absent.

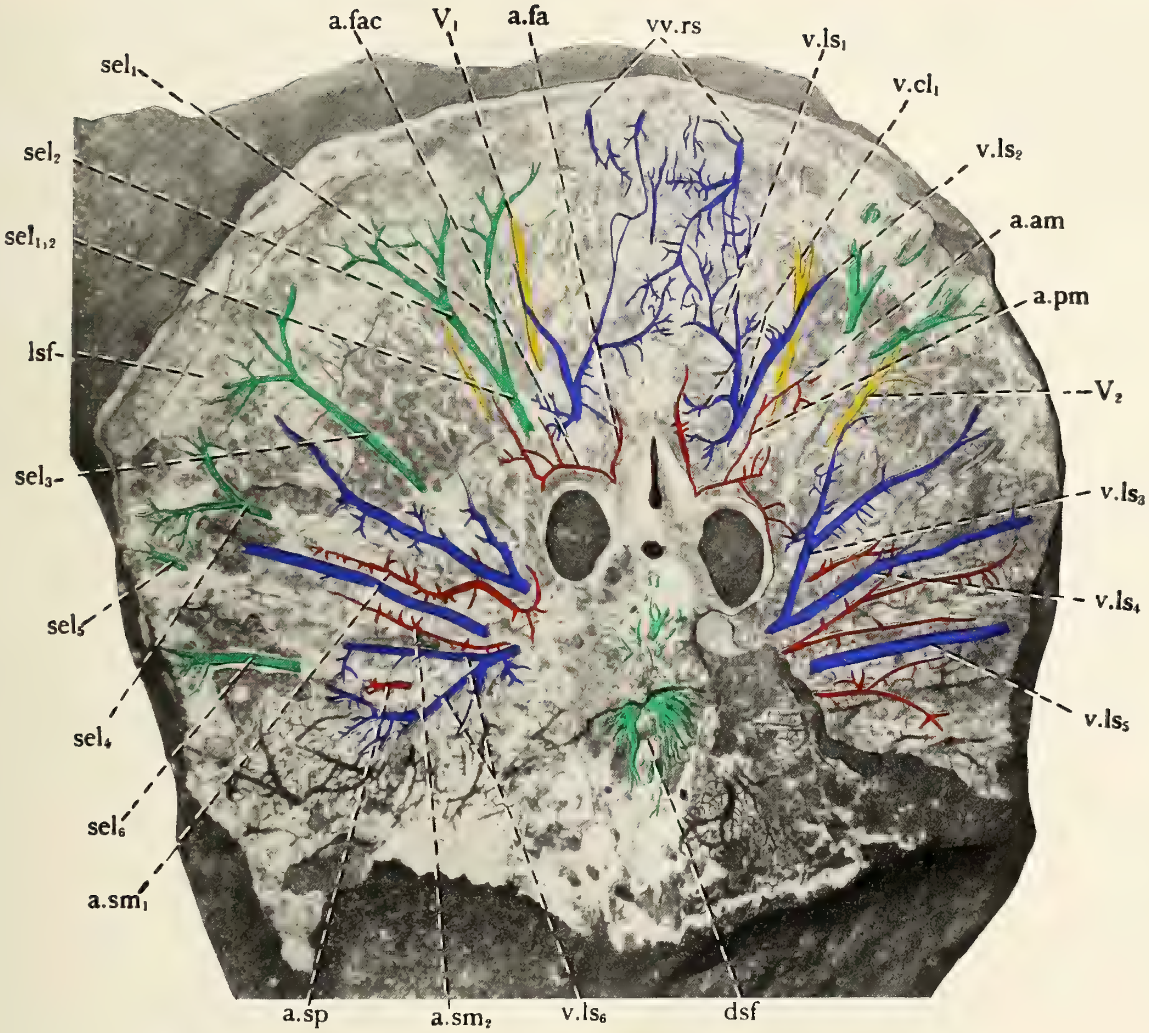
Lateral Sensory Canal System of the Cephalic Shield.

The lateral sensory canal system is, as in the Spitsbergen forms, known only on the dorsal side of the cephalic shield, and is represented in the fossil merely by narrow and very shallow open grooves which may be interrupted in places. These grooves are especially well preserved in *Hemicyclaspis murchisoni* (text-figs. 15, 23, 25; Pl. 1, figs. 1–3; Pl. 3, fig. 4), *Cephalaspis salweyi* (text-fig. 29), *C. pagei* (text-fig. 33A; Pl. 36, figs. 3–5; Pl. 40, fig. 1; Pl. 42, figs. 1, 2; Pl. 43, fig. 1), *C. powriei* var. *brevicornis* (text-fig. 36; Pl. 29, fig. 3), *C. lankesteri* (text-fig. 41; Pl. 17, fig. 3) and *Benneviaspis lankesteri* (text-fig. 55; Pl. 47, fig. 1), but they have been found in a more or less complete state in several other species of *Cephalaspis* (text-figs. 34, 48, 50, 53, 54; Pl. 19, fig. 4; Pl. 20, fig. 1; Pl. 23, fig. 1; Pl. 24, fig. 1; Pl. 31; Pl. 46, figs. 1, 2) and in *Didymaspis grindrodi* (text-fig. 61A; Pl. 55, fig. 3). As a rule they are preserved more often and more completely in those forms in which the superficial parts of the exoskeleton are well developed than in those forms in which these parts are much reduced, although in the latter the lateral sensory canal system was also well developed, and the rarity or absence of grooves on these forms is simply due to the fact that it lay for the most part outside the exoskeleton.

From the position and development of its grooves in the fossils it is evident that the lateral sensory canal system of the Cephalaspids did not lie in the corium but was confined to the epidermis only, and it is therefore most likely that it did not consist of closed canals, but that throughout its extent it was represented by open epidermal grooves. The bottom of these grooves, which certainly lay somewhat lower than the basal surface of the epidermis, gave rise, of course, to the grooves on the exoskeleton wherever the latter reached the most superficial parts of the corium.

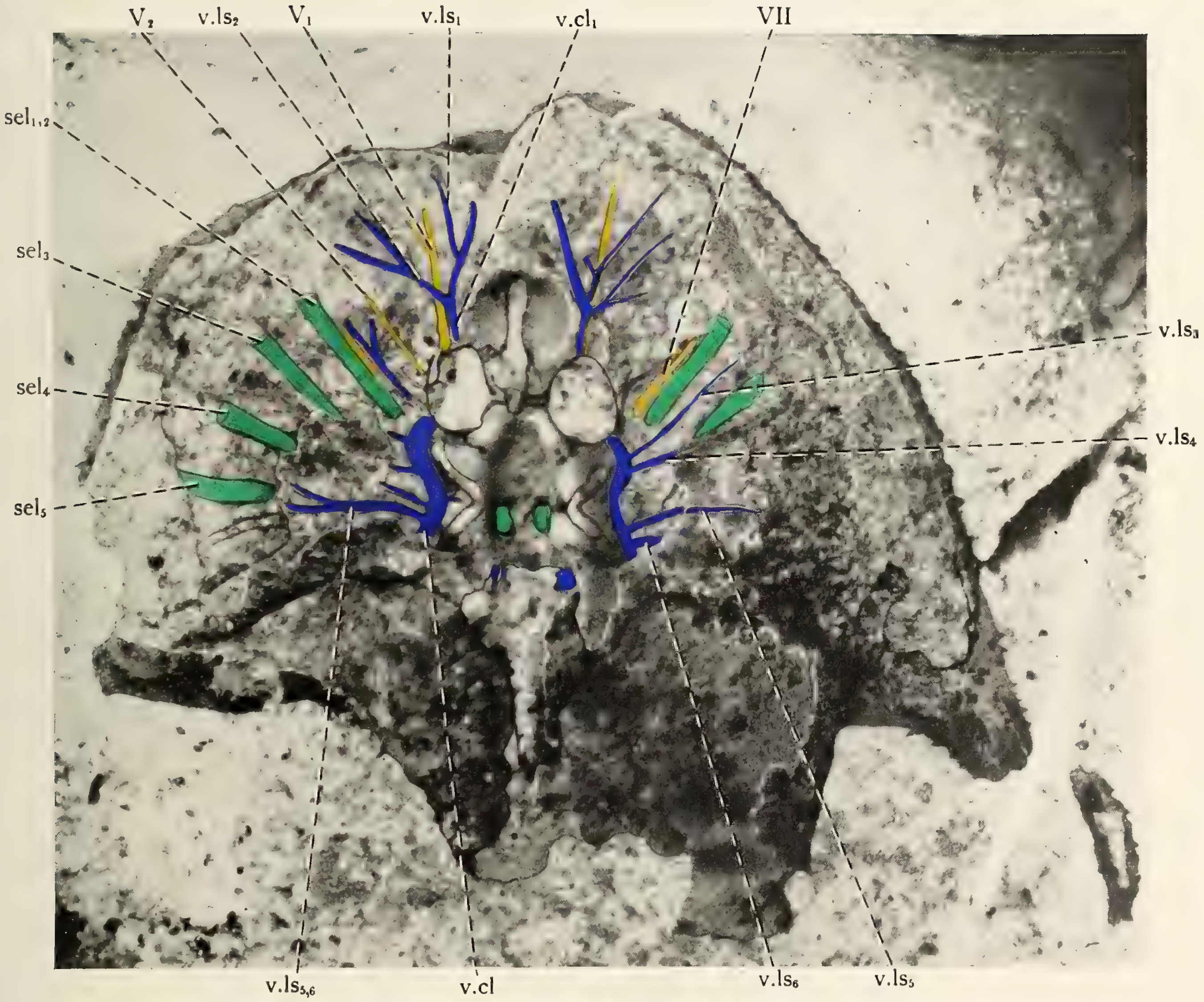
On the whole, the grooves of the lateral sensory canal system of the British Cephalaspids agree with those of the Spitsbergen forms; as, however, they are not only better preserved than in these forms, but also display certain new details of importance, it is necessary to give an extended account of them here.

Each of the pair of infra-orbital grooves (*ifc*, *ifc*$_1$, text-figs. 15, 23, 25, 29, 33A, 34, 36, 41, 50A, 61A; Pl. 1, figs. 1–3; Pl. 2, fig. 4; Pl. 3, fig. 4; Pl. 17, fig. 3; Pl. 20, fig. 1; Pl. 24, figs. 1, 2; Pl. 29, fig. 3; Pl. 31; Pl. 36, figs. 3–5; Pl. 40, fig. 1; Pl. 42, figs. 1, 2; Pl. 43, fig. 1; Pl. 46, figs. 1, 2; Pl. 55, fig. 3) is usually continuous throughout its extent, but in certain cases it may be interrupted at one or more points. According to its course and position, it may be considered to be composed



TEXT-FIG. 12.—*Benneviaspis* sp. System of vascular canals on the dorsal side of the endoskeleton of the cephalic shield. The nerves of the electric fields, green; the ordinary cranial nerves, yellow; the arteries, red; and the veins, blue. After specimen no. 1890$\frac{6}{29}$ *a* in Royal Scottish Museum, Edinburgh (Pl. 48, fig. 1). × 3 diam.

a.am, pre-mandibular branch of the a. facialis; *a.fa*, anterior branch from the a. facialis; *a.fac*, arteria facialis; *a.pm*, pre-mandibular branch of the a. facialis; *a.sm*$_1$, *a.sm*$_2$, *a.sp*, dorso-lateral superficial arteries 2–4; *dsf*, dorsal electric field; *lsf*, lateral electric field; *sel*$_{1,2}$, common trunk of the two most anterior nerves of the lateral electric field; *sel*$_1$–*sel*$_6$, nerves of the lateral electric field; *v.cl*$_1$, pre-orbital division of the v. capitis lateralis; *v.ls*$_1$–*v.ls*$_6$, dorso-lateral superficial veins 1–6; *vv.rs*, rostral veins; V_1, n. profundus; V_2, n. trigeminus proper.



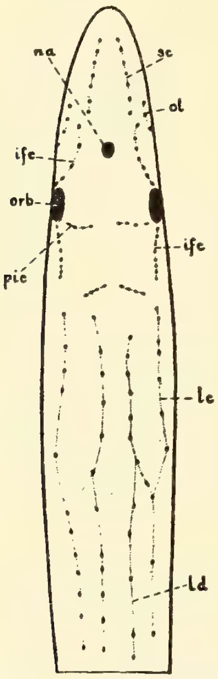
TEXT-FIG. 13.—*Thyestes egertoni* (LANKESTER). Some of the most important venous trunks on the dorsal side of the endo-skeleton of the cephalic shield. The nerves of the electric fields, green; the ordinary cranial nerves, yellow; veins, blue. After specimen no. P. 8831*a* in the British Museum (Pl. 51, fig. 2). × 7 diam.

sel$_{1,2}$, the most anterior electric nerve of the lateral electric field, formed by the union of the two most anterior nerves; *sel*$_3$–*sel*$_5$, the nerves 3–5 of the lateral electric field; *v.cl*, post-orbital division of the vena capitis lateralis; *v.cl*$_1$, pre-orbital division of the v. capitis lateralis; *v.ls*$_1$–*v.ls*$_6$, dorso-lateral superficial veins 1–6; *v.ls*$_{5,6}$, vein probably formed by the union of the dorso-lateral superficial veins 5 and 6; *V*$_1$, n. profundus; *V*$_2$, n. trigeminus proper; *VII*, n. facialis.

of two divisions, a posterior (*ifc*), which runs obliquely outwards and forwards from a point near the outer side of the orbital opening; and an anterior (ifc_1), which as a rule forms the direct continuation of the posterior division, curving forwards and inwards to a point near the median line, not so very far behind the rostral margin of the cephalic shield, or the rostral angle in those species in which this is developed. In *Didymaspis* the two divisions of this groove differ from those in all the other forms in which they are known in that they meet each other at a pronounced angle (text-fig. 61A; Pl. 55, fig. 3), and that the anterior division continues somewhat behind the point at which it joins the posterior. In those species in which the lateral electric field reaches far forwards—that is, in species of *Hemicyclaspis, Cephalaspis, Securiaspis* and *Benneviaspis*—the anterior division is situated with its hinder, and by far the longer, portion lying on the exoskeletal plates of the most anterior part of the lateral electric field, and with its foremost portion situated medially to the anterior end of that electric field; whereas the posterior division lies entirely between the field and the orbit (text-figs. 15, 23, 25, 33, 48, 53, 54). In *Didymaspis,* in which, as we have seen (p. 47), the lateral electric field does not reach so far forward as in the genera just mentioned, the infra-orbital groove is throughout its extent situated in front of, or more exactly, antero-medially to, that field (text-fig. 61A); and, as far as can be judged, a similar arrangement was present also in *Sclerodus* [*Eukeraspis*] and *Thyestes,* although the infra-orbital groove in these was so superficial in position that it gave rise to no impressions on the exoskeleton.

In the Spitsbergen forms only the posterior division of the infra-orbital groove could be seen (*cf.* STENSIÖ 1927, p. 236), but this division was so developed as to make it clear that the anterior division also was generally present and had a distribution similar to that in the British forms. Accordingly, it is probable that in the Cephalaspids in general the infra-orbital groove was developed as in the British forms.

Since the posterior division of the infra-orbital groove follows approximately the course of the canal of the n. trigeminus proper (V_2), it seems very likely that this division was supplied by lateralis fibres which accompanied that nerve, and that these fibres together formed the homologue of the n. buccalis lateralis of fishes. The hinder portion of the anterior division of the infra-orbital groove may very well have been supplied by some of the lateralis fibres which accompanied the n. trigeminus proper; whereas the anterior portion of this division of the infra-orbital groove lies so far forward on the rostral part of the cephalic shield that it seems most probable that it was innervated by lateralis fibres, which we must assume were associated with the n. profundus. If so, the course of the latter fibres was such that they must have corresponded to the n. ophthalmicus lateralis of fishes, and as that is always the special nerve of the supra-orbital sensory canal, this arrangement suggests that the infra-orbital groove may comprise most anteriorly a component which is the homologue at least of the anterior part of the supra-orbital lateral sensory canal of fishes. This is of great interest, for in the Petromyzontids (text-fig. 14) the row of lateral sensory canal organs corresponding to the infra-orbital canal of fishes (*ifc*) begins at a point some way behind the eye, runs on from there forwards and somewhat downwards to the eye itself, and thence for a fair distance in front of the eye on the dorsal side of the head laterally and antero-laterally to the naso-hypophysial aperture, precisely as the infra-orbital groove runs in the Cephalaspids. In front of this row of lateral sensory canal organs there is on the dorsal side of the head of the Petromyzontids another paired row of such organs which ends anteriorly close behind the tip of the snout. This row (*sc*, text-fig. 14) is innervated by lateralis fibres which accompany the n. profundus, and it is therefore probably homologous with the supra-orbital sensory canal of fishes; it seems, therefore, to agree in all characters of importance with the anterior division of the infra-orbital groove of the Cephalaspids, and in any case its relations are such that it must be homologous with that division.



TEXT-FIG. 14.—*Petromyzon fluviatilis* LINNAEUS. The head and branchial region in dorsal view, showing the approximate distribution of the lateral canal sense-organs (neuromasts). The lateral canal sense-organs denoted by large dots. The small dots drawn to show the arrangement of the lateral canal sense-organs in distinct lines (from STENSIÖ 1926).

ifc, infra-orbital line of lateral canal sense-organs; *lc*, main lateral line; *ld*, dorsal lateral line; *na*, naso-hypophysial aperture; *orb*, eye; *pic*, pineal line of lateral canal sense-organs; *ol*, line of lateral canal sense-organs along the mouth opening; *sc*, supra-orbital line of lateral canal sense-organs.

We thus see that in the development of the lateral line system on the rostral part of the head, the Cephalaspids show a much greater degree of resemblance to Petromyzontids than was formerly supposed (*cf.* STENSIÖ 1927, p. 355).

The groove which seems to correspond to either the pre-opercular or jugal canal of fishes (*cm*) is often displayed in the British forms; in many cases this groove is rather short (text-figs. 15, 23, 29, 33A, 36, 41, 55; Pl. 17, fig. 3; Pl. 31; Pl. 36, figs. 3, 4; Pl. 42, fig. 2; Pl. 43, fig. 1; Pl. 47, fig. 1).

The groove which is the homologue of the cephalic division of the main lateral line of fishes (*lc*) is represented in those British forms in which it could be observed (text-figs. 15, 23, 25, 33, 34, 36, 41, 55; Pl. 17, fig. 3; Pl. 31; Pl. 36, fig. 3; Pl. 43, fig. 1; Pl. 46, fig. 2; Pl. 47, fig. 1) only by one or two short anterior segments, which stop considerably before reaching the posterior margin of the cephalic shield, in contrast to that in *Benneviaspis holtedahli* from the Spitsbergen Downtonian (*cf.* STENSIÖ 1927, text-fig. 76A, p. 290).

The short, more or less transverse, groove present in *Tremataspis*, *Benneviaspis holtedahli* and *Hoelaspis angulata* close behind each orbital opening at the lateral border of the dorsal electric field, which is probably the homologue of the supra-pineal canal of the Pteraspids and the pineal line of lateral canal sense-organs of *Petromyzon* (*pic*, text-fig. 14; *cf.* also STENSIÖ 1926, p. 10; 1927, pp. 238, 307), could not be found among the British forms in either *Hemicyclaspis* or *Cephalaspis*, and it is therefore likely that in these it was absent. Whether it was developed or not in the other British forms could not be discovered in the material available for study.

The short transverse groove, which in *Tremataspis*, *Benneviaspis holtedahli* and

Hoelaspis angulata lies close to the lateral margin of the dorsal electric field somewhat behind the one just noted, and which is probably homologous with the middle head-line of pit-organs of fishes, the first cross-commissural canal behind the supra-pineal canal of *Palaeaspis*, and the first transverse line of lateral canal sense-organs behind the pineal line in *Petromyzon* (text-fig. 14; *cf.* also Stensiö 1926, p. 12; 1927, pp. 238, 307), is to be seen in many of the British species (*cmm*, text-figs. 15, 23, 25, 29, 33A, 41, 55; Pl. 17, fig. 3; Pl. 31; Pl. 42, fig. 2; Pl. 43, fig. 1; Pl. 47, fig. 1).

Finally, the long transverse groove which, at least in its most dorso-medial part, is the homologue of the posterior head-line of pit-organs or the supra-temporal cross-commissural canal of fishes, and of the structures corresponding to these in the Pteraspids and in *Petromyzon* (*cf.* Stensiö 1926; 1927, pp. 236–237), is not infrequently present in the British forms ($cmm_1 + cmm_2$ or $cmm_1 + cmm_2 + cmm_3$, text-figs. 15, 23, 25, 33A, 34, 36, 41, 55; Pl. 17, fig. 3; Pl. 31; Pl. 40, fig. 1; Pl. 43, fig. 1; Pl. 46, fig. 2; Pl. 47, fig. 1). In *Cephalaspis powriei* (Pl. 31), *C. spinifer* (text-fig. 34; Pl. 46, fig. 2) and in *C. pagei* (text-fig. 33A; Pl. 43, fig. 1) it clearly begins on the exoskeletal plates of the dorsal electric field, and, at least in some forms, it extends ventro-laterally on to the zonal (shoulder-girdle) part of the cephalic shield. In all the species in which it is known so far it is subdivided into two or more parts which may be of varying lengths.

For other details concerning the lateral sensory canal system of the Cephalaspids the reader is referred to my monograph on the Spitsbergen forms (Stensiö 1927, pp. 235–238, 306, 308, 355).

TRUNK

Division of the Trunk included in the Cephalic Shield

As was shown in the description of the Spitsbergen forms (Stensiö 1927, pp. 19–28) and has also been emphasized in the present work in the general description of the cephalic shield (pp. 4, 7–10), this shield is not limited by the head only, but includes also a division which belongs to the trunk; and, as we have also seen, this trunk or abdominal division is composed of a paired lateral area, the zonal or shoulder-girdle part, and an unpaired median area, the inter-zonal part, which as a rule reaches backwards beyond that of the shoulder-girdle. Since the latter has been already described in detail (pp. 7–10, 47), the following account will be confined to the inter-zonal part only.

In most British forms the inter-zonal part is short, or at least not especially long, being composed of rather few segments (*cf.* pp. 8–9); but in *Didymaspis*, on the contrary, it is strikingly long, so long that the scale-covered division of the trunk behind it can have comprised little more than the caudal region (text-fig. 61A, B; Pl. 52, fig. 5; Pl. 54, figs. 1, 3, 4; Pl. 55, figs. 1–4). Anteriorly it passes over without any boundary into the cephalic division of the cephalic shield, whereas posteriorly it narrows and gradually assumes the shape of the scale-covered division of the trunk.

In *Hemicyclaspis* and most species of *Cephalaspis* its cross-section posteriorly has the shape of a fairly high, more or less rounded, isosceles triangle, with the base ventral and the dorsal apex represented by the angle formed by the median dorsal ridge, or spine where this is developed. In *Benneviaspis, Securiaspis, Didymaspis* and perhaps also in *Thyestes,* such a cross-section seems also to have had the shape of an isosceles triangle, but is much lower, so that the breadth is equal to or exceeds the height.

Posteriorly the exoskeleton of the inter-zonal part is not always sharply divided from the scale-covered division of the trunk, but in most forms there is a certain transitional area between them. Thus, as we have seen (pp. 8–9), it has scales belonging to different transverse rows incorporated with it at different heights, and ventrally it may even be represented, as in *Hemicyclaspis murchisoni,* by independent skeletal plates which are continued forwards by the plates of the ventral visceral exoskeleton and backwards by the ordinary ventral trunk-scales.

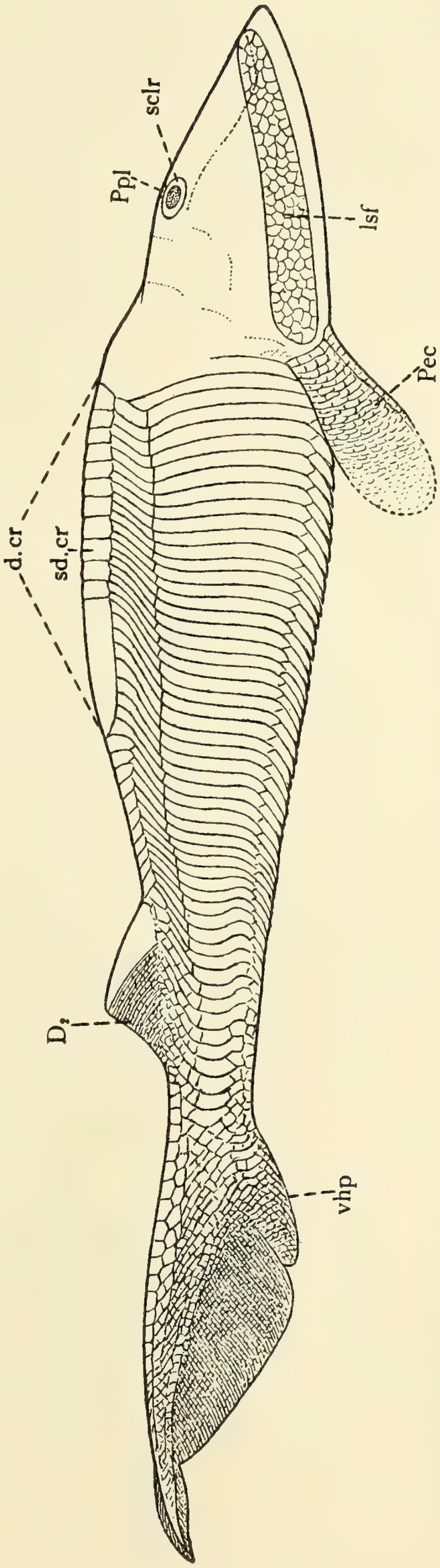
Division of the Trunk following the Cephalic Shield

General shape.—Whereas in the Spitsbergen forms the cephalic shield was usually the only part of the skeleton preserved, we find not infrequently in the British material remains of the scale-covered division of the trunk as well as the cephalic shield.

In *Hemicyclaspis murchisoni* (text-figs. 15, 23, 25, 26; Pl. 1, figs. 1, 2; Pl. 2, figs. 2–4; Pl. 3, figs. 1–4; Pl. 4, figs. 1, 2; Pl. 5, figs. 1–4; Pl. 6, figs. 1–3; Pl. 7, figs. 1, 3–5; Pl. 8, fig. 1) the trunk division is highest and broadest in its anterior third, decreasing from there backwards both in height and breadth. From its anterior boundary as far backwards as a point somewhat in front of the caudal fin it is distinctly three-sided, the form being roughly that of an isosceles triangle with the base ventral and the apex dorsal (text-fig. 26A–C). The ventral surface, which is broad and markedly concave (text-fig. 26A–C; Pl. 3, fig. 3; Pl. 4, figs. 1, 2), is throughout its extent separated from each side by a pronounced ridge, the *ventro-lateral ridge,* which will be described in greater detail in the account of the squamation and in the description of the fins. The lateral surfaces meet dorsally in a pronounced ridge, the *dorsal ridge,* which in the anterior third of the division is elevated into a fairly high crest, the *dorsal crest* (*d.cr,* text-figs. 15, 23, 25, 26; Pl. 1, fig. 2; Pl. 2, fig. 4; Pl. 3, fig. 4), forming a direct posterior continuation of the dorsal median crest of the cephalic shield and, as we shall see, probably representing the reduced and much-transformed anterior dorsal fin. The lateral surfaces, it should be mentioned here, are convex throughout their extent, though their degree of convexity diminishes markedly towards the tail (text-fig. 26A–C). The most posterior part of this division of the trunk in *Hemicyclaspis murchisoni,* namely, that situated between the second dorsal fin and the caudal fin (text-figs. 15, 25, 26D; Pl. 2, fig. 4; Pl. 3, fig. 4; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 7, fig. 4), is decidedly higher than broad. Its ventral surface is probably not distinctly bounded and is moderately convex. The lateral surfaces in this region seem to meet dorsally in a fairly distinct dorsal ridge, while a cross-section is probably less distinctly triangular or perhaps in its hindmost parts almost oval in shape (text-fig. 26D).

The anal opening of *Hemicyclaspis murchisoni* (*an*, Pl. 4, fig. 1) is a transverse slit placed some distance in front of the posterior end of the ventral surface and of the ventro-lateral ridges.

In *Cephalaspis* the scale-covered division of the trunk agrees well in general shape with the corresponding division in *Hemicyclaspis murchisoni* (Pl. 14, figs. 2–4; Pl. 22, fig. 6; Pl. 25, fig. 3; Pl. 28, fig. 3; Pl. 30, figs. 1, 3, 4; Pls. 31, 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 3; Pl. 36, fig. 3; Pl. 37, figs. 2, 3; Pl. 38, figs. 1, 3, 4; Pl. 39, figs. 1, 2; Pl. 40, figs. 1, 3; Pl. 43, figs. 1, 2; Pl. 46, figs. 1, 2); but in *Benneviaspis, Securiaspis, Didymaspis* and *Sclerodus* [*Eukeraspis*] this division has not so far been found preserved. Despite this, it is possible to draw certain conclusions about its shape in these genera. In *Benneviaspis, Securiaspis* and *Sclerodus* it was evidently of much the same relative length as in *Hemicyclaspis* and *Cephalaspis*. In *Didymaspis*, on the contrary, it must certainly have been much shorter and represented by hardly more than the caudal region; for in this genus the part incorporated in the cephalic shield is, as we have already seen (*cf.* pp. 51–52), so long that it undoubtedly comprises almost the entire abdominal region. As in *Benneviaspis, Securiaspis* and *Didymaspis* the interzonal part of the cephalic shield is low and fairly broad, it seems most likely that the scale-covered division of these genera throughout its length was shaped accordingly.



Text-fig. 15.—*Hemicyclaspis murchisoni* (Egerton). Restoration in lateral view. Chiefly after specimen no. P. 6023 (I) in the British Museum. Nat. size. *D_2*, dorsal fin; *d.cr*, dorsal crest of trunk; *lsf*, lateral electric field; *Pec*, pectoral fin; *Ppl*, pineal plate; *sclr*, sclerotic ring; *sd.cr*, dorsal scutes; *vhp*, ventral axis of the caudal fin, perhaps representing the vestigial axis of an originally hypocercal caudal fin.

In *Thyestes,* in which remains of the anterior parts of it have been found preserved (text-fig. 60; Pl. 40, fig. 2; Pl. 51, fig. 3), it is clear that the scale-covered division was fairly low and broad, and that in addition it was devoid of the dorsal crest so well developed in *Hemicyclaspis* and *Cephalaspis.* The dorsal ridge in *Thyestes,* though much flattened, continues forwards as far as the posterior angle of the cephalic shield: otherwise this division in *Thyestes* seems, so far as known, to agree fairly well with that in *Hemicyclaspis* and *Cephalaspis.*

Finally, the scale-covered division of the trunk is partly preserved in *Ateleaspis.* In this genus, however, it is so much compressed and in such a poor state of preservation that it can only be said that it was fairly long and probably like that in the other Cephalaspids.

Squamation.—The scales covering the division of the trunk behind the cephalic shield are here referred to as *trunk-scales.* For the study of these scales we shall first turn to *Hemicyclaspis murchisoni,* in which the squamation is better and more completely preserved than in any of the other British species of which material is available.

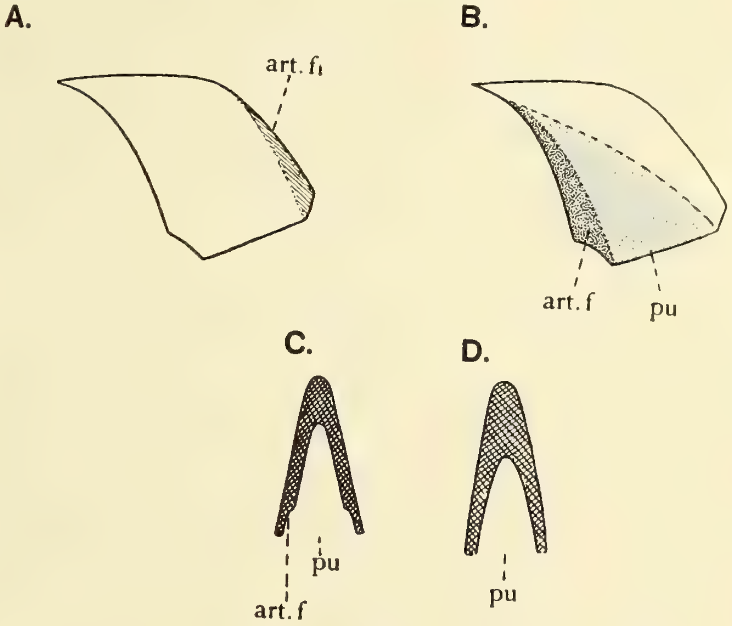
In *Hemicyclaspis murchisoni* we may distinguish the following kinds of scales: (1) the scutes of the dorsal crest, (2) the dorsal ridge-scales and fulcral scales, and (3) the scales of the lateral and ventral surfaces.

The scutes (*sd.cr,* text-figs. 15, 16, 23, 25, 26A, B; Pl. 2, figs. 2–4; Pl. 3, figs. 1, 2, 4) occur only in the dorsal crest, which in the fossil condition is formed entirely by them. They are all unpaired. Their exact number cannot be made out in any of the specimens available, but as far as can be seen it must have been between 12 and 14. The most posterior scute is very long, about five times as long as high, but with this exception they are all either somewhat shorter than high or else approximately square. The most posterior scute seems to have had no internal cavity and was probably connected by a simple suture with the one next in front. The second scute probably had a small cavity in the interior of its basal part and articulated by means of a special articular surface on its anterior margin with that preceding it, by which it was to a certain extent overlapped. The third scute from behind is shaped like the second, but has a fairly considerable cavity in its interior, a cavity (*pu,* text-fig. 16B–D; Pl. 2, figs. 2, 3) which reaches to its posterior dorsal corner and opens posteriorly. Along the posterior border of each side of this cavity there is a distinct facet (*art.f*) for articulation with the anterior margin of the scute next behind, and a corresponding facet is present on the anterior margin of the third scute ($art.f_1$, text-fig. 16A) for articulation with that next in front. The scutes preceding this one agree in all respects with it, but the articular surfaces are usually longer and much more distinctly developed.

We thus find the scutes of the dorsal crest have an imbricating arrangement and, with the exception of the two most posterior, they meet each other in distinct articulations. As we shall see from the account of the fins below, these scutes are probably the vestiges of the much-reduced and transformed anterior dorsal fin, which is present in certain forms (text-figs. 21, 22), and we may note that these scutes are in position, shape and structure suggestive of the dorsal spines of the *Anaspida* (Kiaer 1924, pp. 62–63, 96).

The dorsal ridge-scales of *Hemicyclaspis murchisoni* are unpaired scales which cover the dorsal ridge of the trunk posteriorly to the dorsal crest (text-figs. 15, 25, 26C, D; Pl. 2, fig. 4; Pl. 3, fig. 4; Pl. 5, fig. 1; Pl. 7, fig. 4; Pl. 8, fig. 1). From this crest they reach backwards to the anterior margin of the extant dorsal fin, and then from the posterior margin of that fin to the very tip of the caudal fin, on which they become completely fulcrum-like, and may, indeed, be termed fulcra. They are smaller than the scutes of the dorsal crest, but otherwise seem to be essentially the same. Thus they probably have a cavity in their interior which, like those in the scutes, is open downwards and posteriorly; and they have probably also a similar imbricating arrangement and mode of articulation with each other.

Finally, the scales of the lateral and ventral surfaces of *Hemicyclaspis murchisoni* are arranged in paired rows running more or less at right angles to the longitudinal axis of the trunk, which we will therefore term *transverse rows* (text-figs. 15, 23, 25; Pl. 1, figs. 1, 2; Pl. 2, figs. 1–4; Pl. 3, figs. 1–4; Pl. 4, figs. 1, 2; Pl. 5, figs. 1–4; Pl. 6, figs. 1–3; Pl. 7, figs. 1, 3–5; Pl. 8, fig. 1).



TEXT-FIG. 16.—*Hemicyclaspis murchisoni* (EGERTON). Middle scute of the dorsal crest. A, in lateral profile; B, in lateral profile but with the extent of the interior cavity indicated by shading; C, most posterior cross-section; D, anterior cross-section. All × 6 diam.

art.f, *art.f*$_1$, surfaces for articulation with the scutes behind and in front. The surface for the articulation with the scute behind (*art.f*) is situated on the side of the internal cavity and its extent forward is indicated in fig. B by a dotted line; *pu*, cavity in the interior of the scute.

For the detailed study of these transverse rows of scales in *Hemicyclaspis murchisoni* we first turn to the posterior part of the caudal region. Here these rows begin immediately below the dorsal ridge-scales (the fulcral scales). Just in front of the caudal fin they are somewhat irregularly developed, and further backwards, on the axis[1] of the caudal fin, they do not quite reach the membrane of that fin, but are separated from it by a longitudinal series of scales suggestive of the series of small 'lancet-shaped' scales described by KIAER in the caudal fin of the Anaspids. In some specimens, at least, they are also separated dorsally from the fulcra by one or two irregular longitudinal series of scales which also resemble somewhat the 'lancet-shaped' scales of the Anaspids. On the axis of the caudal fin the transverse rows are, moreover, characterized by a gradual decrease in their breadth towards the tip of the tail, by their oblique arrangement downwards and forwards, and by the fact that they consist chiefly of small scales more or less rhomboid in shape. From this it is obvious that the axis of the caudal fin of *Hemicyclaspis murchisoni* in its squamation generally resembles the Palaeoniscids and other *Chondrostei,* but that it has also distinct Anaspid-like characters.

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[1] By axis is meant the main axis only.

On the rest of the tail and trunk in *Hemicyclaspis murchisoni* the transverse rows of scales are always well developed. They begin dorsally immediately under the scutes of the dorsal crest and the dorsal ridge-scales, and reach so far downwards that they come into contact with those of the opposite side at the mid-line of the ventral surface, where they alternate with each other (text-fig. 8; Pl. 3, fig. 3; Pl. 4, figs. 1, 2; Pl. 6, fig. 1; Pl. 7, figs. 3, 5). Each row comprises a dorsal scale which is inclined forward; this is succeeded ventrally by one which is very deep and more or less vertical, followed by a scale which forms part of the ventro-lateral ridge. Finally, there is a ventral portion which lies on the under surface of the trunk and meets that of the opposite side in mid-line. We shall now deal with each of these portions in detail.

The uppermost series of forwardly inclined scales varies somewhat in its development in different places (*dls,* text-figs. 15, 17, 23, 25; Pl. 2, figs. 2–4; Pl. 3, figs. 1, 2, 4; Pl. 5, fig. 2; Pl. 7, fig. 1; Pl. 8, fig. 1; Pl. 65, figs. 2, 3): thus, between the cephalic shield and the second dorsal fin it consists as a rule of only one or two fairly high scales, but as these, owing to certain rostro-caudal lines of weakness in their structure, are usually fractured in several places, this row appears to consist of about three or four, or perhaps even more, scales (in Pl. 65, figs. 2, 3, these lines of fracture are well shown). Under the second dorsal fin it seems to consist of fairly numerous, somewhat irregularly shaped scales; this appearance may to a certain extent be due to fractures, but it is likely that there are here a number of independent scales. Finally, behind the second dorsal fin this series seems to consist of a few independent scales. The subdivision and comparative irregularity in arrangement of these upper scales below the second dorsal fin are certainly due to the movement of this fin requiring greater flexibility in the exoskeleton there than in front or behind. The scales of this series, on account of their position on the trunk, will in future be referred to as the *dorso-lateral scales.*

The deep vertical series decreases gradually in height from in front backwards, but despite this the scales are still fairly high in the caudal region. Ventrally it reaches down almost to the ventro-lateral ridge, and in most rows it consists only of a single, very high scale (*ls,* text-figs. 15, 17, 23, 25; Pl. 1, fig. 1; Pl. 2, fig. 4; Pl. 3, figs. 1, 2, 4; Pl. 5, fig. 2; Pl. 7, figs. 1, 4, 5). Like the dorso-lateral scales, these scales are not infrequently subdivided into two or more by means of rostro-caudal fractures along structural lines of weakness. Seen from the front or from behind they appear in all the rows convex on the outer side and correspondingly concave on the inner; whereas viewed laterally they appear fairly straight in the most anterior rows, but in the more posterior they gradually become sigmoidally curved, the upper end being directed somewhat forwards and the lower end somewhat backwards. The scales of this series of the transverse rows will be called the *lateral scales.*

Each row of the underlying series consists of a dorsal part situated on the lateral surface of the trunk and a ventro-lateral part which is indistinct and merely forms an angle just behind the cephalic shield, but which more posteriorly is developed as an outwardly projecting process. These ventro-lateral parts, the *ventro-lateral processes,* together form the *ventro-lateral ridge,* which extends backwards considerably beyond the anal opening (Pl. 4, fig. 1) and thus into the caudal region. The ventro-lateral portion of the first few transverse rows behind the cephalic shield may consist of two, or perhaps even more, scales, but more posteriorly it always consists of one scale only (*vrs,* text-figs. 8, 15, 17; Pl. 1, figs. 1, 2; Pl. 3, figs. 1–4; Pl. 4, figs. 1, 2; Pl. 7, figs. 1, 3, 5). The scales of this portion of the vertical rows we shall refer to as the *ventro-lateral scales,* and, as we shall see below, their structure indicates that we are probably concerned with skeletal elements of a paired fin-fold (*cf.* the description of the micro-structure of the scales and the account of the paired fins below).

Lastly, the ventral portions of the transverse rows of scales decrease in length as the trunk diminishes in breadth towards the tail. Each row is always narrower near the mid-line of the ventral surface than near the ventro-lateral ridge. In one or two instances the rows immediately behind the cephalic shield curve backwards and consist of numerous and mostly rather small scales, the most median of which are somewhat irregularly developed so that they form a transitional stage between the plates representing the ventro-median portion of the inter-zonal part of the cephalic shield and the ordinary median scales of the ventral surface. In a fair number of rows following the two most anterior, this ventral portion on each side is divisible into two parts, of which the outer (or lateral) curves inwards and backwards, and a much narrower, median part forms a forwardly directed chevron with the corresponding scale of the other side. In the remaining, posterior, rows the lateral part gradually changes its direction to one more or less parallel with the median part. In the anterior rows following behind the first two or three the number of scales is probably about seven or eight, but the number decreases somewhat towards the rear, so that behind the anal opening it is probably only four.[1] The scales of this portion of the transverse rows, which will be termed the *ventral scales,* are somewhat irregularly developed only in front of the anal opening and to a certain extent behind it: otherwise they are all approximately rectangular and wider than long. That the most median scales of the right side alternate with the corresponding scales of the left side is clearly seen in several specimens (*vs,* text-fig. 8; Pl. 3, fig. 3; Pl. 4, figs. 1, 2; Pl. 6, figs. 1–3; Pl. 7, figs. 3, 5).

To sum up, we may distinguish in each transverse row of scales in front of the extreme caudal region in *Hemicyclaspis murchisoni* one or more dorso-lateral scales; one high lateral scale; one, and in front perhaps two or more, ventro-lateral scales; and finally a number of ventral scales.

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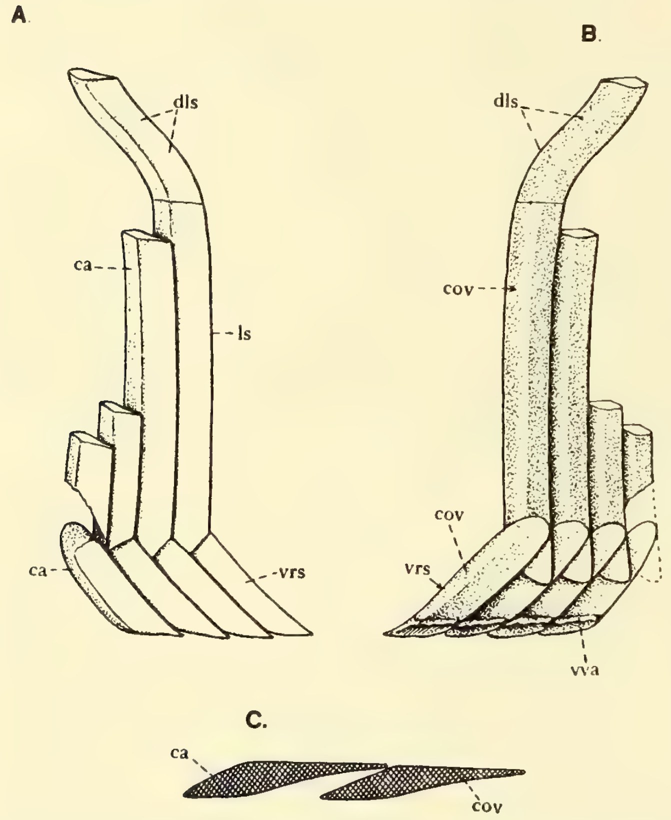
[1] It is not unlikely that the number of scales given here may be greater than the actual number, for the ventral scales are certainly broken along lines of weakness in a way similar to the dorso-lateral and lateral scales, but owing to the state of preservation it was impossible to be certain of their arrangement in this region.

The dorso-lateral scales (*dls*, text-fig. 17A, B) were probably attached by their dorsal margins to the ventral margins of the scutes of the dorsal crest anteriorly and of the dorsal ridge-scales posteriorly; but in any case it is certain that there was no distinct articulation here. When there were two or more dorso-lateral scales in the same transverse row, these did not articulate with each other, but were connected simply by sutures.



Text-fig. 17.—*Hemicyclaspis murchisoni* (Egerton). Portion of the lateral squamation from the middle part of the trunk; A, outer view; B, inner or medial view; C, diagrammatic transverse (horizontal) section showing articulation of scales. Approx. × 2 diam.

ca, area covered by the scale in front; *cov*, area covering the succeeding scale; *dls*, dorso-lateral scales; *ls*, lateral scales; *vrs*, ventro-lateral scales; *vva*, ridge by means of which the ventro-lateral scales were connected with the ventral scales.

The lateral scale (*ls*, text-fig. 17; Pl. 2, fig. 2; Pl. 7, fig. 1) of each transverse row is attached to the corresponding dorso-lateral scale by a suture only, and in some rows they are incompletely separated. On the other hand, ventrally the lateral scale was movably articulated both with the ventro-lateral scale of its own row and with that of the row immediately in front: that is, it is overlapped at its antero-ventral corner by the ventro-lateral scale of the row in front and itself overlaps the dorsal end of that of its own row (text-fig. 17A, B; Pl. 7, fig. 1).

For articulation with the lateral scale of its own row each ventro-lateral scale (*vrs*, text-fig. 17A, B; Pl. 7, fig. 1) has a special area on the outer surface of its dorsal end, an area which is continuous with the area for articulation with the ventro-lateral scale of the row next in front of it. As is seen from a dorso-ventral section (text-fig. 18A), these scales are confined in *Hemicyclaspis murchisoni* to the lateral surface of the trunk and to the ventro-lateral ridge, and thus cover little of the ventral surface of the trunk. As far as can be judged, it was connected to the ventral scale of its own row by means of a suture only, and in any case it is evident from its mode of articulation with this scale that it was but slightly movable. Immediately behind the cephalic shield, where there are sometimes two or more ventro-lateral scales in each row, the mode of articulation could not be clearly ascertained.

Finally, the ventral scales in each row of *H. murchisoni* are connected with each other by sutures only. Those which lie nearest the ventral mid-line meet their corresponding scales of the other side in a movable articulation, but how this articulation was developed exactly it is difficult to discover from the material available; but it seems likely that each scale of the one side articulated with two scales of the other side (*vs*, text-fig. 8; Pl. 4, fig. 1; Pl. 6, fig. 1; Pl. 7, figs. 3, 5).

The scales in each transverse row in *H. murchisoni* are overlapped anteriorly by those of the row in front and themselves overlap the scales in the row behind them. They have, therefore, an overlapped area along the anterior margin of their lateral (outer) surface (*ca*, text-fig. 17) and an overlapping area along the posterior margin of their medial (inner) surface (*cov*, text-fig. 17). The overlapped area (*ca*), which is always devoid of the superficial layer, may be fairly broad, and in the lateral scales it constitutes about one-third of the total breadth of the scale. The overlapping area (*cov*), which is even broader, is in the form of a groove that is usually very shallow (text-fig. 17). On account of the presence of this groove, the scales, which gradually decrease in thickness towards the tail, finally become almost as thin as a membrane.

In *Cephalaspis* the squamation is in all essentials similar to that in *Hemicyclaspis murchisoni*[1] (Pl. 14, figs. 2–4; Pl. 22, fig. 6; Pl. 25, fig. 3; Pl. 28, fig. 3; Pl. 30, figs. 1, 3, 4; Pls. 31, 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 3; Pl. 36, fig. 3; Pl. 37, figs. 2, 3; Pl. 38, figs. 1, 3, 4; Pl. 39, figs. 1, 2; Pl. 40, figs. 1, 3; Pl. 43, figs. 1, 2; Pl. 46, figs. 1, 2), but the ventro-lateral scales, at least in some species, are not confined to the ventral part of the lateral surface of the trunk and to the ventro-lateral ridge, but cover also the marginal area of the ventral surface of the trunk (text-fig. 18B, C), and in addition the lateral scale of each row immediately below the second dorsal fin is subdivided. The scutes of the dorsal crest and the dorsal ridge-scales in all true species of *Cephalaspis* are developed as in *Hemicyclaspis murchisoni*, but it should be noted that in some of the species from the Spitsbergen Downtonian which have been referred to *Cephalaspis*, the scutes of the dorsal crest are represented by an anterior dorsal fin which is covered by fairly large, scale-like plates (text-fig. 22; *cf.* also pp. 67–69).

The squamation is also partly known in *Thyestes egertoni*. In this species, as has already been mentioned (text-fig. 60; Pl. 40, fig. 2; Pl. 51, fig. 3), the dorsal crest was not developed, and consequently there are no dorsal scutes, but the dorsal ridge-scales continue forwards to the posterior margin of the cephalic shield. These ridge-scales are strikingly broad and flat. In several of the anterior transverse rows the dorso-lateral scale is coalesced with the lateral, giving rise to a single, very high scale reaching from the dorsal ridge-scale downwards to the ventro-lateral scale, which, however, is badly preserved in all specimens yet seen, so that nothing is known of its details. The ventral scales are so far unknown.

From the above account it seems likely that the transverse rows of scales are so developed that they corresponded both in number and shape to the myomeres of the trunk; in any case it is evident that they must reflect to some extent the general shape of the myomeres in their arrangement and curvature.

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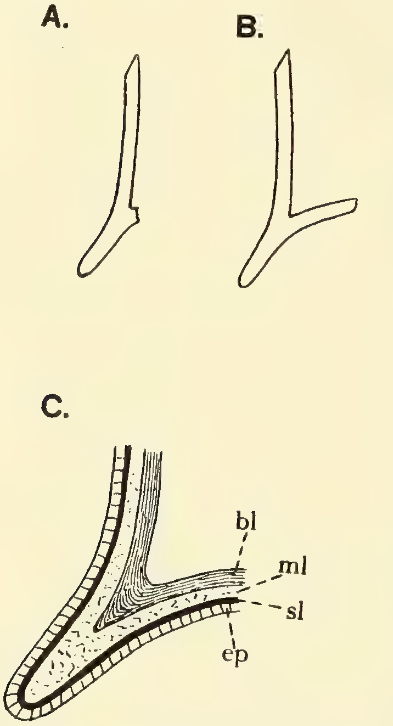
[1] That is, so far as it is known; but our knowledge of the squamation of the ventral surface of *Cephalaspis* is very imperfect.

We may note here that, despite certain obvious differences, the squamation of the Cephalaspids as a whole bears a distinct resemblance to that of the Anaspids (*cf.* Kiaer 1924, pp. 96–97). This resemblance is further discussed below.

Micro-structure of the scales.—The trunk-scales are of the same thickness as the exoskeleton of the cephalic shield, and, like this, they were developed in the corium, which they represent in its entire, or almost entire, thickness. These scales consist of a basal layer, a middle layer and a superficial layer, which in all essentials agree with the corresponding layers in the exoskeleton of the cephalic shield (*cf.* pp. 13–27).

The basal layer is always well developed and, like that in the cephalic shield, is perforated by ascending vascular canals (*c.asc*, text-fig. 19; Pl. 57, fig. 1; Pl. 65, fig. 2). The middle layer is likewise rich in canals, and radiating canals are very well developed in it, at least in *Hemicyclaspis* and *Cephalaspis* (*rad.c*, text-fig. 19; Pl. 57, fig. 1; Pl. 65, fig. 2). In species in which this layer is more or less reduced in the exoskeleton of the cephalic shield, it is also correspondingly reduced in the scales; and on the covered areas of the scales it is absent, at least along the anterior border. Finally, the superficial layer is present only on the exposed areas of the scales, where in each form of Cephalaspid it is developed to the same extent as on the cephalic shield. The ornamentation of the scales in the various species also seems to agree with that of the cephalic shield.

The relations of the three layers of the ventro-lateral scales are of much interest, and we shall therefore deal with their structure here in greater detail.



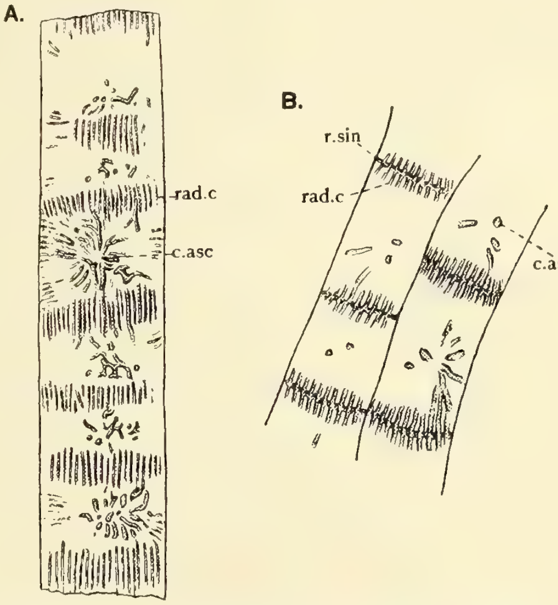
Text-fig. 18.—Diagrammatic sketch of a vertical section through ventro-lateral scales of A, *Hemicyclaspis murchisoni* (Egerton); B, *Cephalaspis pagei* Lankester; C, restoration showing the relations of a ventro-lateral scale to the epidermis. *ep*, epidermis; *bl*, basal layer; *ml*, middle layer; *sl*, superficial layer.

As shown by text-fig. 18, the dorsal part of the ventro-lateral scale situated on the side of the trunk, and the ventral part of the same scale situated on the ventral surface (when developed), both have the normal structure of the scales, whereas the ventro-lateral process of the scales situated in, and forming part of, the ventro-lateral ridge exhibits certain differences. Thus internally this process is composed almost entirely of the middle layer (*ml*), the basal layer (*bl*) extending only for a short distance into the most proximal part: the superficial layer (*sl*) is, however, continuous and forms a complete covering.

It is evident from their structure that the processes of these scales forming the ventro-lateral ridge were situated in a fold of the skin in such a way that they were completely covered by the epidermis (text-fig. 18C). It is therefore clear that the ventro-lateral ridge supported a paired longitudinal fold of the skin, a fold which, as we shall see from the account given below (*cf.* pp. 64–67), was the most distal part of a greater fold that affected not only the skin but also certain of the structures beneath it.

The mucous canal system was present not only on the cephalic shield, but also on the scale-covered division of the trunk and on the pectoral fins. On the squamation of the trunk it could be studied only in *Hemicyclaspis murchisoni* and *Cephalaspis pagei.*

In *H. murchisoni* this system always consists of fine, uniformly developed canals (*mc,* Pl. 65, figs. 2, 3), which are enclosed within the scales, forming a fine-meshed plexus. These canals, among which it is impossible to distinguish the inter- and intra-areal series, are arranged mainly in two directions: rostro-caudally and dorso-ventrally. The former are fairly long, sometimes so long that they reach right across the exposed part of the scales; whereas those directed dorso-ventrally are, on the contrary, always short. Owing to this development, the meshes of the mucous canal system are as a rule considerably broader than high, and the system itself has the appearance of being composed mainly of canals arranged rostro-caudally.



Text-fig. 19.—*Hemicyclaspis murchisoni* (Egerton) Sketches showing the arrangement of the radiating vascular canals. A, in a part of a lateral scale; B, in the middle part of two dorso-lateral scales. Approx. × 10 diam.

c.asc, ascending vascular canals; *rad.c*, radiating vascular canals; *r.sin*, venous sinus corresponding to the ring-sinus of the cephalic shield.

In *C. pagei* the mucous canals of the scale-covered division of the trunk are arranged in much the same way as in *H. murchisoni*, but whereas in the latter species they are always closed canals, in *C. pagei* they are thus developed only in certain specimens, while in others they are more or less shallow, open grooves: or, expressed in another way, in some specimens of *C. pagei* they lie completely enclosed in the scales, but in others they lie more or less superficially to them. However, the mucous canals in *C. pagei* always agree in their development with those of the cephalic shield, which is to say that they are developed as closed canals when those of the cephalic shield are closed canals, but as more or less shallow and indistinct grooves when those of the cephalic shield are represented by such grooves. In certain specimens of *C. pagei* they may even resemble those of the cephalic shield in being partly of the one type and partly of the other; and such an example is met with in the specimen figured in Pl. 22, fig. 6, in which the canals in question are closed where the external surface of the scales is smooth, but occur as open grooves where the external surface is striated.[1]

The vascular canals of the scales of *H. murchisoni*, *C. pagei* and *C. powriei* are, like the vascular canals of the exoskeleton of the cephalic shield of these species, arranged into distinct vascular areas (text-fig. 19; Pl. 57, fig. 1; Pl. 65, figs. 2, 3); and this was certainly the case in the Cephalaspids in general. In each vascular area we may distinguish, as in the cephalic shield, ascending vascular canals (*c.asc*), radiating vascular canals (*rad.c*) and, when the superficial layer is continuous, also external branches from the radiating canals. Whereas the radiating canals in the cephalic shield in each polygonal area issue from the centre of their area in fascicles towards each of the adjacent polygonal areas, we find here in the scales that they issue merely in two directions, dorsally and ventrally, to the adjacent polygonal areas situated in the same transverse row of scales. Between the vascular areas, and thus in an inter-areal position, there are in the basal layer of the scales fairly wide rostro-caudal canals (*r.sin*, text-fig. 19B; Pl. 63, fig. 3) which are in communication with the radiating canals by means of descending vascular canals, and thus appear to be identical both in position and function with the ring-sinuses of the cephalic shield. On account of this they will here be termed ring-sinuses, although they are not ring-shaped.

The number of vascular areas, and thus also the number of polygonal areas, in the scales of *H. murchisoni*, *C. pagei* and *C. powriei* varies from one to about ten or twelve in each scale, according to its height. In the other Cephalaspids the number is not exactly known, but it is likely that in them it was about the same in the highest scales.[2]

The ring-sinuses do not occur between all the vascular areas, but they are nevertheless not rare, and the dorso-lateral and especially the lateral scales are usually pierced by them in two or more places. Together with the descending canals leading down to them, the ring-sinuses form, of course, lines of considerable weakness in the basal parts of the scales where they occur between the vascular areas, and owing to this the scales are often fractured across. Since these fractures are difficult to distinguish from real interspaces between scales in the same transverse row, the taller scales especially give at first sight the impression that they are not single units but consist of a number of smaller scales.

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[1] In those places where the external surface of the scales is smooth, the superficial layer is present as a continuous covering to the middle one; where striation is to be seen, the superficial layer is present only in somewhat elongated tubercles or short ridges (Pl. 22, fig. 6).

[2] In *Sclerodus* [*Eukeraspis*] the vascular canals of the scales, like those of the cephalic shield, were probably not arranged in vascular areas.

FINS

Paired Fins

Pectoral fins.—The pectoral fins have been found preserved in *Hemicyclaspis murchisoni* and in several of the species of *Cephalaspis* (*Pec*, text-figs. 15, 23, 25; Pl. 1, figs. 1, 2; Pl. 2, figs. 1, 4; Pl. 3, fig. 4; Pl. 4, fig. 2; Pl. 7, fig. 3; Pl. 8, fig. 3; Pl. 28, fig. 3; Pl. 30, figs. 1, 4; Pl. 31; Pl. 37, fig. 3; Pl. 40, fig. 1; Pl. 43, figs. 1, 2), but in no other forms have remains of them yet been discovered. In *Hemicyclaspis murchisoni,* in which they are best preserved, they are fairly large and paddle-shaped; in the species of *Cephalaspis* they are also large, and everything seems to indicate that in these species they were of approximately the same shape as in *Hemicyclaspis.* In such forms as *Didymaspis,* in which there are only very small pectoral sinuses (text-fig. 61; Pl. 52, fig. 5; Pl. 54, figs. 1–4; Pl. 55, figs. 1–4), they must, of course, have been much smaller than in *Hemicyclaspis* and *Cephalaspis.*

In *Hemicyclaspis murchisoni* and in *Cephalaspis* the pectoral fin has no typical lepidotrichia, but is covered by imbricating scales. On the proximal part of the fin these scales are fairly large and arranged in more or less distinct, transverse rows, but towards the tip of the fin they gradually decrease in size, finally becoming so small that they appear as small tubercles which are hardly visible to the naked eye. In *Hemicyclaspis murchisoni* (text-figs. 15, 23, 25; Pl. 1, figs. 1, 2; Pl. 2, fig. 1) the marginal scales of the proximal part of each fin form a distinct series. Along the lateral part of each fin in *Cephalaspis powriei* there are several strong, rounded tubercles which seem to have belonged to the lateral part of the fin (Pl. 30, fig. 4; Pl. 43, fig. 2). How these tubercles were arranged cannot, however, be established with certainty.

Whether the pectoral fin in genera other than *Hemicyclaspis* and *Cephalaspis* was provided with scales cannot be definitely decided at present; but it does not seem improbable that in some forms it may have lost its squamation or have had scales too delicate to be preserved except under extraordinarily favourable conditions.

The scales of the pectoral fin in *Hemicyclaspis* and *Cephalaspis* (Pl. 8, fig. 3) consist of the same three layers as the rest of the exoskeleton (*cf.* pp. 13–27). All but the smallest of these scales are perforated by a group of ascending vascular canals which, in the central parts of their respective scales, break up into radiating canals (*rad.c*) in the normal way. Contrary to what is the case in the trunk-scales, these radiating canals do not issue in two directions only, but towards all the adjacent scales, as in the polygonal areas of the cephalic shield, thus corresponding exactly in micro-structure to a polygonal area in the exoskeleton elsewhere.

In *H. murchisoni,* in which the scales of the pectoral fin are best preserved and always provided with a continuous superficial layer (*sl*, Pl. 8, fig. 3), it is clearly seen that this layer is perforated by pores belonging to the mucous canal system, and it is therefore evident that the system is also present on the pectoral fin of *Cephalaspis.* How this system was developed in the fin could not, however, be established with certainty, but it is obvious that its intra-areal canals in *H. murchisoni* lie within, and the inter-areal canals at least partly between, the larger scales.

The pectoral fin exhibits no remains of an ossified or calcified endoskeleton, but it is very likely that an endoskeleton was present, probably of some sort of cartilage.

As noted above, the pectoral fin lacks typical lepidotrichia arranged as external fin-rays. The absence of these is not, however, so remarkable as it perhaps would seem, for in several forms the exoskeleton of the other fins does not comprise distinct lepidotrichia but instead more or less typical scales; and this is true also of the entire anal fin and a part of the caudal fin in the *Anaspida* (Kiaer 1924, pp. 72–80, text-figs. 33–37). We may note in this connection that there is no fundamental difference between lepidotrichia and scales (Goodrich 1904; 1906; 1908; 1909, p. 212), for typical lepidotrichia arise ontogenetically as rows of ordinary scales and thus certainly must have originated phyletically from scales. The absence of typical lepidotrichia in the pectoral fin of the Cephalaspids is therefore no evidence against this fin being a real pectoral fin.

If we take into consideration the facts that the pectoral fin is situated behind the branchial chamber, that it articulates with that part of the cephalic shield which seems to correspond to the shoulder-girdle of fishes and higher vertebrates, and that its nerve- and blood-supply was probably essentially similar to that of the pectoral fin of fishes, the interpretation given here of this fin is, at the moment, the only possible one.

Though the pectoral fin is shown in the figure which Agassiz published in 1837 of the type of *Cephalaspis lyelli* (*Poiss. Foss.*, Tome II, Part I, Pl. 1*a*, fig. 2), strangely enough it was not mentioned in the text. The first to give a description of it and to interpret it as a pectoral fin was Powrie in 1861 (p. 138). Lankester, who in 1870 (p. 41) dealt with it in greater detail, seems to have felt a little uncertain whether he really was dealing with the pectoral fin, for he alternately refers to it as a " strange pectoral organ " and " fin," and says that it " may have had other functions than that of mere locomotion," adding that, from its position, to him it did not at all seem improbable that it " may have been efficient in causing currents of water to pass to the branchial organs covered in by the great head-shield." This opinion of its respiratory function was adopted by Woodward in 1891 (pp. 186–187), who thought that he had found certain evidence that it was not a fin but an operculum (*cf.* also Woodward 1898, p. 10; 1921, p. 32). Traquair (1899*b*, p. 858) was inclined to look upon it as a pectoral fin; Koken (1911, pp. 33–34) and Schlosser (1918, p. 33; 1923, p. 34) were uncertain whether it really was an operculum or a pectoral fin; finally, Jaekel (1902, p. 111; 1911, p. 33), Patten (1903*a*, pp. 849–851) and Kiaer (1924, pp. 100–101) arrived at the conclusion that it really was homologous with the pectoral fin, and the researches carried out by the present writer both in 1927 (Stensiö 1927, pp. 231–235, 244) and in the present work seem to confirm fully this conclusion.

Ventral fins.—As is well known, a real ventral fin is not present in the Cephalaspids. The ventro-lateral part of the trunk behind the cephalic shield, however, is so developed that it is of much interest in this connection.

In *Hemicyclaspis murchisoni* (text-figs. 15, 25, 26; Pl. 3, fig. 3; Pl. 4, figs. 1, 2, Pl. 7, figs. 1, 5), in which, as pointed out (p. 52), the ventral surface behind the cephalic shield is decidedly concave in cross-section, the ventro-lateral part of each side of the trunk, from close behind the pectoral fin almost as far backwards as the caudal fin, protrudes as a thick fold—a fold which has not only influenced the skin but also several structures beneath it, among others probably the somatic musculature. This ventro-lateral fold was protected in *Hemicyclaspis murchisoni* by the ventro-lateral scales and the most lateral of the ventral scales. The projecting parts of the ventro-lateral scales—the ventro-lateral processes—forming the ventro-lateral ridge in the fossil (*cf.* pp. 57, 59–61), were, of course, enveloped in skin which projected ventro-laterally beyond them as a mere flap (the epidermis *plus* the corium).

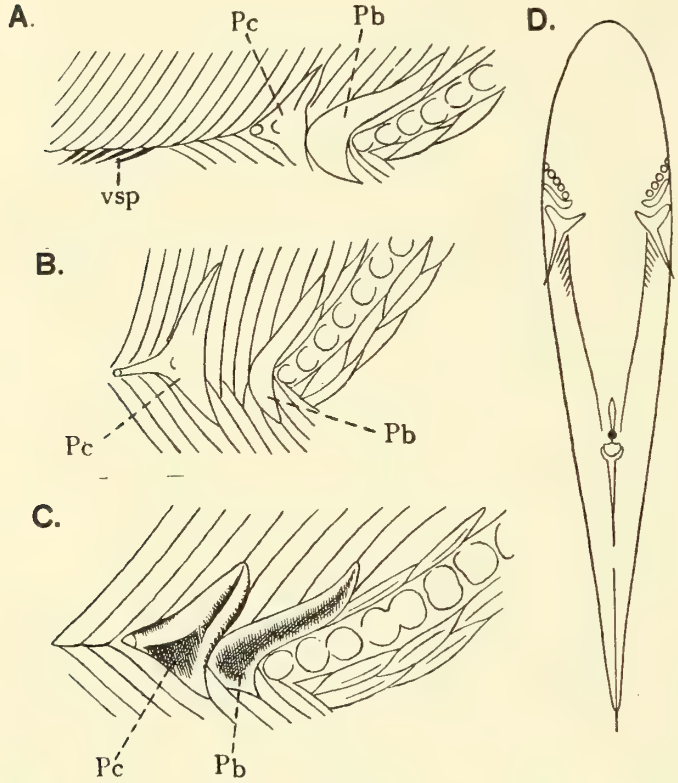
Judging from what is known in the other Cephalaspids, it seems certain that in these also a somewhat similar, thick ventro-lateral fold was developed, and thus it is probable that such a fold was present in all Cephalaspids. In the species of *Cephalaspis* in which the details are known this fold was protected, however, only by the ventro-lateral scales, which in these species also cover the marginal areas of the ventral surface of the trunk (*cf.* pp. 57, 59–61).

In position and extent the ventro-lateral fold of the Cephalaspids bears a superficial resemblance to the metapleural fold of *Amphioxus*, but the latter ends close behind the atrial pore, far in front of the anal opening, and is thus confined to the respiratory region of the trunk; whereas the ventro-lateral fold of the Cephalaspids begins behind both the gills and the pectoral fins and, moreover, reaches far behind the anal opening. It is thus evident that the ventro-lateral fold of the Cephalaspids cannot be homologous with the metapleural fold of *Amphioxus*.

On the other hand, as emphasized by Kiaer (1924, pp. 100–101), the ventro-lateral fold of the Cephalaspids is very suggestive in its position, extent and anatomical relations of the paired fold from which the ventral fins of fishes develop during ontogeny (*cf.* Braus 1904, pp. 196–212), and, as in addition it is sometimes developed most strongly just in front of the anal opening, everything seems to indicate that it really is the homologue of the ventral fin of fishes. Thus, if this theory is true, we are here concerned with a ventral fin in a very primitive stage of development.

It may also be emphasized here that in those Cephalaspids in which the anterior dorsal fin has not entirely disappeared but is represented by a dorsal crest (*cf.* pp. 54–55, 67–69), this consists also of a fold supported by strong scutes, most of which are hollow like the ventro-lateral scales of species in which these scales surround the entire ventro-lateral fold (*cf.* text-figs. 15, 16; Pl. 2, figs. 2–4; Pl. 3, fig. 4). Accordingly, we find that one of the unpaired fins may under certain conditions be transformed into a crest-like fold closely resembling the ventro-lateral fold; and we have in this fact an additional support for the idea that the ventro-lateral folds really may be considered to represent fins, and to be homologous with the ventral fins.

A fact which is also of much interest in this connection is that, as was shown by Kiaer (1924, pp. 70–71, 99–105; *cf.* also Stetson 1927; 1928*a*, pp. 459–461), the *Anaspida* possess structures which are very suggestive of the ventro-lateral scales of the Cephalaspids and which, like them, must have originated in a pair of ventro-lateral folds of the trunk (text-fig. 20). These structures are the post-branchial plate, the pectoral plate and the ventro-lateral spines in *Birkenia, Pterolepis, Rhyncholepis* and *Pharyngolepis,* and the post-branchial rods in *Lasanius.* And it is not difficult to see that in general shape, structure and position in relation to the trunk-scales, the post-branchial plate and the pectoral plate each correspond fairly well to a whole ventro-lateral scale of the Cephalaspids, whereas the ventro-lateral spines following behind the pectoral plate are comparable merely to the ventro-lateral processes of the ventro-lateral scales of the Cephalaspids (text-fig. 20). Whilst these structures of the Anaspids begin immediately behind the branchial openings and reach only a short distance backwards, the ventro-lateral scales of the Cephalaspids begin first behind the shoulder-girdle component of the cephalic shield and the pectoral fin, but reach instead much further backwards. As pointed out by Kiaer, the fold in which the structures of the Anaspids arose must, on account of its position far forward, have represented the pectoral fin of fishes and Cephalaspids, whereas the ventro-lateral fold of the Cephalaspids in which the ventro-lateral scales are situated seems to be equivalent to the ventral fin of fishes. Accordingly, in the Anaspids the pectoral fin would be represented by a ventro-lateral fold of a type essentially similar to that of the ventral fin in the Cephalaspids, and thus we find here conditions which seem to indicate that in the common ancestors of the Anaspids and Cephalaspids the pectoral and ventral fins of each side were both represented by folds which lay in a straight line with one another and were probably continuous. If it really was so, we would have had in the primitive ancestors of the Anaspids and Cephalaspids a paired fin-fold in such a primitive stage of development that it corresponded exactly to the paired fold from which, according to the fin-fold theory, the paired fins developed (*cf.* Goodrich 1930, pp. 123–144). In the Cephalaspids, then, the anterior part of this fold would have become strongly developed and transformed into a paddle-like pectoral fin, whereas the posterior



Text-fig. 20.—*Pterolepis nitidus* Kiaer. A–C, pectoral spine apparatus in lateral view. × 3–4 diam. D, sketch of the animal in ventral view. Nat. size. After Kiaer 1924.

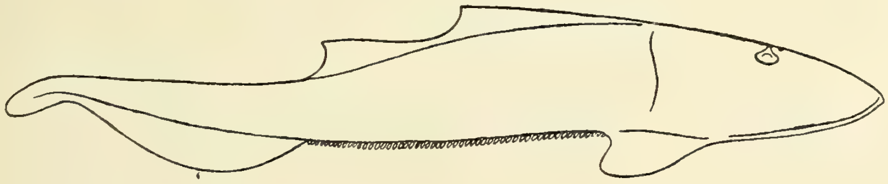
Pb, post-branchial plate; *Pc*, pectoral plate; *vsp*, ventro-lateral spines.

part remained more or less unchanged. In the Anaspids, on the contrary, the anterior part would have remained unchanged or somewhat reduced, whilst the posterior part became entirely reduced.

The first to point out that the ventro-lateral scales of the Cephalaspids were of importance from a morphological point of view was PATTEN (1903*a*, pp. 851–856). PATTEN at that time, however, compared them to the abdominal appendages of the Arthropods. The first really to perceive the true nature of these scales and to advance the view that they were situated in a paired fin-fold was, as already mentioned above in this chapter, KIAER in 1924 (pp. 100–101). And, as we have seen from the above facts, everything known so far seems to support his opinion.

Unpaired Fins

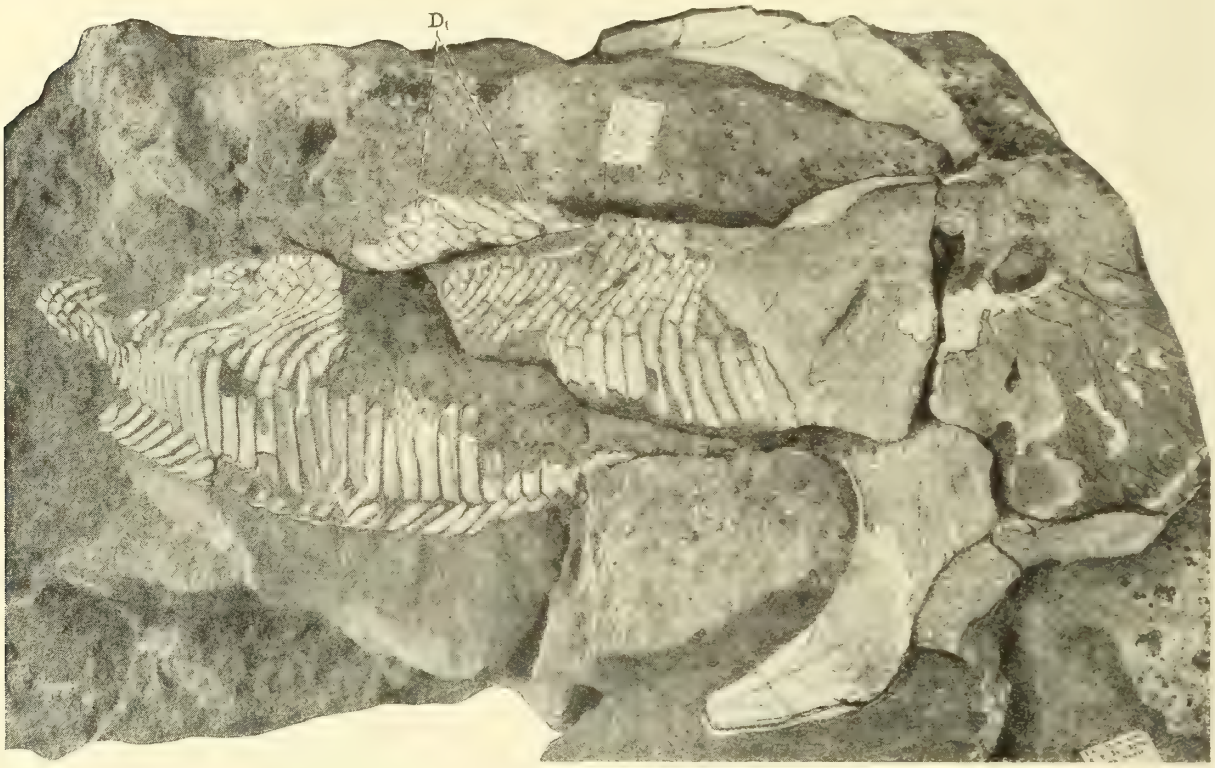
Dorsal fins.—In certain of the Downtonian Cephalaspids, such as *Aceraspis robusta* (text-fig. 21) from Norway (KIAER 1924, text-fig. 45) and a *Cephalaspis*-like species from Spitsbergen (text-fig. 22), there are two dorsal fins, anterior and posterior, distinctly developed.



TEXT-FIG. 21.—*Aceraspis robusta* KIAER. Sketch showing the general shape of the animal. Nat. size. After KIAER 1924.

In both *Aceraspis* and this *Cephalaspis*-like species from Spitsbergen the anterior dorsal fin (D_1, text-figs. 21, 22) begins immediately behind the cephalic shield. In *Aceraspis,* in which the cephalic shield seems to lack a dorsal spine, the fin follows immediately behind and forms the direct posterior continuation of the dorsal median crest of the cephalic shield; in the *Cephalaspis*-like species from Spitsbergen, in which the cephalic shield seems to have been provided with a dorsal spine of moderate size, this spine certainly lay in, and formed the anterior border of, the fin in question. Thus in both these forms the anterior dorsal fin has immediately in front of it a ridge or a spine on the posterior part of the cephalic shield, and, as the posterior dorsal fin also has the anterior margin strengthened by a spine, it seems possible that the ridge or the spine which usually occurs on the dorsal side of the cephalic shield really belongs to the anterior dorsal fin. According to the sketch published by KIAER of *Aceraspis robusta* (text-fig. 21), the anterior dorsal fin in this species seems to be continuous with the posterior, being marked off from this only by an emargination in the continuous fin-membrane of the two fins. Whether the arrangement was similar in the *Cephalaspis*-like species from Spitsbergen cannot be ascertained, as its posterior dorsal fin is not preserved.

In *Hemicyclaspis murchisoni* and in all the British species of *Cephalaspis* no real anterior dorsal fin is to be found (see pp. 54–55). Instead of this fin, however, there is a pronounced crest—the dorsal crest—which extends from the median dorsal crest, or the dorsal spine, of the cephalic shield for a considerable distance backwards, but not as far as the posterior dorsal fin (*d.cr*, text-figs. 15, 23, 25; Pl. 2, figs. 2–4; Pl. 3, figs. 1–3; Pl. 30, fig. 1; Pl. 31; Pl. 35, fig. 3). In the fossil state this crest (see p. 54) is formed by a series of unpaired and fairly high scutes (*sd.cr*, text-figs. 15, 16, 25; Pl. 2, figs. 2, 3), which, with the exception of the most posterior, are imbricating and hollow in their interior. This series of scutes ends abruptly behind in such a way (text-figs. 15, 25; Pl. 2, figs. 2–4; Pl. 3, fig. 4; Pl. 35, fig. 3) that it must clearly be of a different nature from the other series of scales of the trunk. The most posterior of the scutes seems as a rule to be much longer than the others, all of which are either somewhat higher than long, or else almost rhombic in shape when seen from the side. From their structure it is quite evident that these scutes lay in, and formed the exoskeleton of, a fairly high fold—the dorsal fold. This fold, like the anterior dorsal fin of *Aceraspis robusta* and the *Cephalaspis*-like species from Spitsbergen, surely formed the direct posterior continuation of the dorsal median crest, or the dorsal spine, of the cephalic shield; for its scutes are evidently of a different nature from the other scutes of the trunk, and in all other respects it



TEXT-FIG. 22.—*Cephalaspis*-like species from the Downtonian of Spitsbergen. The specimen shows part of the anterior dorsal fin (D_1). Original in the Paleontologisk Museum, Oslo. × ¾ diam.

seems to correspond to the anterior dorsal fin of the species just referred to: it can, therefore, hardly be doubted that, with its scutes, it was the homologue of the dorsal fin.

In *Thyestes egertoni* there is no typical anterior dorsal fin, nor any dorsal crest, nor any scutes belonging to such a crest; accordingly, there is no evidence whatever of an anterior dorsal fin in this species (Pl. 40, fig. 2; Pl. 51, fig. 3). It is very likely that this fin was entirely absent also in the other species of *Thyestes* and in the genera most closely allied to *Thyestes*.

Thus there is in certain Downtonian Cephalaspids a well-developed anterior dorsal fin, which in *Hemicyclaspis murchisoni* and in the Devonian species of *Cephalaspis* is represented in the fossil condition only by a pronounced dorsal crest. This crest consists of a series of unpaired dorsal scutes posteriorly to the cephalic shield and of the dorsal crest, or the dorsal spine, on the cephalic shield. Judging from this it seems probable that the anterior dorsal fin in *Hemicyclaspis murchisoni* and the Devonian species of *Cephalaspis* has become reduced and secondarily transformed into the dorsal crest. In its structure and the form of its scutes this crest is very suggestive of the ventro-lateral ridge, which seems to represent the ventral fin of fishes (pp. 64–67). In the Cephalaspids we thus find that both unpaired and paired fins may be represented in the fossil condition by strong crests or ridges strengthened by hollow scales or other hollow exoskeletal structures, and which in the living animals certainly were strong folds that influenced not only the dermal but also other more deeply seated structures. Accordingly, there were in the Cephalaspids true fin-folds representing both unpaired and paired fins.

The posterior dorsal fin (D_2, text-figs. 15, 25; Pl. 2, fig. 4; Pl. 3, fig. 4; Pl. 8, fig. 1; Pl. 16, fig. 1; Pl. 22, fig. 6; Pl. 25, fig. 3; Pls. 31, 33; Pl. 35, fig. 3; Pl. 38, figs. 3, 4; Pl. 39, figs. 1, 2; Pl. 43, fig. 2) has so far been observed in *Aceraspis*, *Hemicyclaspis* and *Cephalaspis* and in these genera it is always fairly small and lies far backwards. Its anterior border is, at least in *Hemicyclaspis* and *Cephalaspis*, strengthened by a spine which in *Hemicyclaspis* is entire, but in certain species of *Cephalaspis* (*C. pagei*, *C. powriei*) is composed of a number of independent, fulcrum-like scales of large size.

The exoskeleton of the anterior dorsal fin is known only in the *Cephalaspis*-like species from Spitsbergen (text-fig. 22), in which it consists of fairly large, scale-like plates; but the exoskeleton of the second dorsal fin, as far as it is known, always consists of very small scales, which in certain species are arranged in vertical rows, forming closely set, primitive lepidotrichia, whereas in others this arrangement is absent.

Caudal fin.—The caudal fin, which is strongly developed, is of the normal heterocercal type (*C*, text-figs. 15, 25; Pl. 2, fig. 4; Pl. 3, fig. 4; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 7, fig. 4; Pl. 8, fig. 1; Pl. 16, fig. 1; Pl. 22, fig. 6; Pl. 25, fig. 3; Pls. 31, 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 3; Pl. 39, figs. 1, 2; Pl. 40, fig. 1; Pl. 43, fig. 1; Pl. 46, figs. 1, 2). The axis of the trunk extending into it is long and seems to reach backwards to the tip. Besides this axis, which we may term the main axis, we find both in *Hemicyclaspis murchisoni* and in several species of *Cephalaspis* definite traces of a ventral axis (*vhp*, text-figs. 15, 25; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 33; Pl. 34, figs. 1, 2; Pl. 43, fig. 1) which forms the support of a more or less independent lobe of the caudal fin-membrane. According to information kindly given me by the late Professor Kiaer, such a ventral axis is entirely absent in the Cephalaspids from the Norwegian Downtonian.

The squamation of the main axis of the fin is developed in a rather complicated way. From above downwards it consists of the following rows of scales:—(1) a fulcral row, which forms the posterior continuation of the dorsal ridge-scales; (2) a few irregularly longitudinal rows, which seem to form the direct continuation below of the fulcral scales and consist of fairly large scales, but are probably not always distinctly developed; (3) a dorsal longitudinal row consisting of small, low scales, which, like the row just mentioned, may often be absent; (4) backwardly inclined dorso-ventral rows of scales, which are developed in the main like the scales on the axis of the tail of Palaeoniscids and other *Chondrostei*; (5) finally, a ventral longitudinal row of scales separating the backwardly inclined rows of scales from the membrane of the fin below, and probably not occurring in all species. The dorsal and ventral longitudinal rows of scales are suggestive of the similarly arranged rows of "lancet-shaped" scales of the Anaspids (*cf.* Kiaer 1924, pp. 74–78, figs. 34C, 35 and 37). Despite the fact that the squamation of the axis as a whole is of Palaeoniscid type, it thus shows quite distinctly certain Anaspid-like characters.

The squamation of the ventral axis of the fin (Pl. 5, fig. 1; Pl. 34, figs. 1, 2; Pl. 43, fig. 1) is much less perfectly known than that of the main axis, but at least in the few cases in which it has been found preserved it seems to consist of rows of scales which are somewhat inclined backwards.

The membrane of the caudal fin consists in *Hemicyclaspis* and *Cephalaspis* of three lobes: the apical lobe, the main lobe, and the antero-ventral lobe. The apical lobe was supported by the very tip of the main axis, and seems to have been developed on both its dorsal and ventral sides. The main lobe was supported by the main axis in front of the apical lobe, and it thus lay entirely on the ventral side of the main axis. Finally, the antero-ventral lobe was supported by the ventral axis of the fin, and it is worthy of notice that it was always more or less independent of the main lobe (Pl. 5, fig. 1; Pl. 33; Pl. 34, figs. 1, 2).

All these lobes of the fin-membrane of the tail were stiffened with scales. The scales of the apical lobe are so fine that their detailed arrangement cannot be ascertained. The scales of the main lobe are in some species arranged in fairly distinct rows perpendicular to the main axis of the fin, giving rise to closely set, primitive lepidotrichia; whereas in other species they seem to have had no such distinct arrangement. Finally, the scales of the antero-ventral lobe are mostly imperfectly preserved, so that their arrangement cannot be made out with certainty; but it is evident that to a large extent they pass gradually into the scales of the ventral axis and that anteriorly a few of them, at least in certain forms (Pl. 34, figs. 1, 2), may be high and arranged in backwardly inclined rows.

The occurrence of the small ventral axis and the antero-ventral lobe in the otherwise typically heterocercal caudal fin of *Hemicyclaspis* and *Cephalaspis* is a character of much interest. As no anal fin is found otherwise in the Cephalaspids, the idea readily suggests itself that the ventral axis of the caudal fin together with its fin membrane represents an anal fin. This seems the more likely if we take into account that a well-developed anal fin, situated far back and rather close to the caudal fin, is present in the closely allied Anaspids. Another suggestion as to the nature of the ventral axis and its lobe that also deserves to be taken into account is that this axis may possibly be the vestigial remains of a once strongly developed ventral axis, in which case the caudal fin originally would have been hypocercal, as in the Anaspids and Petromyzontids. On account of the imperfect state of preservation in which the caudal fin is always found it is difficult to decide, however, which of these suggestions is the more likely.

The anal fin.—An anal fin is not present—at least not as an independent fin—but, as just pointed out, it is not impossible that it may be fused with, and form part of, the caudal fin.

SENSORY CANAL SYSTEM OF THE TRUNK

No sensory canals or grooves have been observed so far on the squamation of the Cephalaspids. This, however, is probably due to the imperfect state of preservation in which the squamation of the Cephalaspids is generally found.

MUCOUS CANAL SYSTEM

From the account given above of the micro-structure of the exoskeleton (pp. 13–27) we have seen that the Cephalaspids, with the probable exception of *Sclerodus* [*Eukeraspis*], are equipped with a special system of canals which I have referred to as the "mucous canal system," since it is homologous to the canal system of *Tremataspis* described under that term by PATTEN (1912, pp. 290–292, figs. 193–195; *cf.* also STENSIÖ 1927, pp. 32–40). This system of canals in the Cephalaspids was, as in *Tremataspis*, situated in the corium; and in those places where the corium was ossified it came, therefore, to be related to the exoskeleton. Since it lay somewhat superficially in the corium, it became entirely enclosed in the exoskeleton only where the superficial parts of the exoskeleton were completely developed. On this account it is represented in the fossil condition by closed canals in the exoskeleton where the superficial layer is present as a continuous covering to the middle layer, but only by more or less indistinct grooves on the exoskeleton where the superficial layer of this is subdivided into tubercles between which the middle layer also has been partly reduced. In forms such as *Thyestes* and *Didymaspis*, in which not only the superficial, but also the middle, layer of the exoskeleton has become very much reduced, it was even situated entirely outside the exoskeleton, so that it gave rise to neither grooves nor markings.

Where the mucous canal system of the Cephalaspids is entirely enclosed in the exoskeleton, it is possible to see that the majority of its canals are situated superficially to the sub-epidermal vascular plexus, between this and the superficial layer of the exoskeleton, but that its widest canals often reach deeper down, sometimes even down to the radiating vascular canals (*mc, iac, ita,* text-figs. 6, 7; Pl. 44, fig. 1; Pl. 59, fig. 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3; Pl. 65, fig. 1). It can also be established that this system was supplied with blood from the sub-epidermal vascular plexus, as several branches ascend to it from the canals of this plexus (*ebc,* text-figs. 6, 7; Pl. 57, fig. 1; Pl. 60, figs. 2–4; Pl. 64, fig. 3) and open into the basal parts of its canals. All its canals open outwards by means of numerous fairly wide pores (*p,* text-figs. 6, 7; Pl. 9; Pl. 36, fig. 4; Pl. 42, fig. 1, at *a*; Pl. 44, fig. 1; Pl. 56, fig. 2; Pl. 57, figs. 2, 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3; Pl. 65, fig. 1) which are enclosed in the exoskeleton so as to pierce the superficial layer and open on its outer surface. Superficially to the exoskeleton these pores certainly also pierced the epidermis.

Where the superficial parts of the exoskeleton are imperfectly developed, the pores lay entirely in the soft tissue which represented the superficial parts of the exoskeleton, and hence no traces of them are to be found in the fossils.

As the various canals or grooves of the mucous canal system do not end blindly when they reach the borders of the various skeletal plates in or on which they are found, but are always open, it is obvious that the mucous canals were not confined to those parts of the corium in which the exoskeleton was developed, but that they were present also in the entirely soft parts of the corium situated between. Accordingly, the mucous canal system was continuous throughout the corium; and, as we have seen, it was developed on the head, on the shoulder-girdle, on the squamous division of the trunk, and also on the pectoral fins.

From their position and development it is obvious that the various canals of the mucous canal system were lined by the epidermis, or, in other words, that they were tubes of the epidermis submerged in the corium.

After the general account of the mucous canal system just given we shall now deal briefly with the arrangement and relations of the various canals of this system.

In the mucous canal system of the Cephalaspids we may distinguish two kinds of mucous canals, inter-areal and intra-areal canals, both of which also occur in *Tremataspis* (*cf.* pp. 16–23; *cf.* also Stensiö 1927, pp. 38–39, Pl. 72, figs. 1, 2).

The inter-areal canals are best known in the cephalic shield. When they are typically developed there (*iac,* text-figs. 5A, B, H, 6; Pl. 4, fig. 3; Pl. 9; Pl. 10, figs. 2, 3; Pl. 24, figs. 1, 2; Pl. 32, fig. 1; Pl. 42, fig. 1; Pl. 45, fig. 3; Pl. 56, fig. 3; Pl. 64, figs. 2, 3) they are fairly wide and form a plexus of large mesh with one another, thus subdividing the superficial parts of the exoskeleton into polygonal areas. The inter-areal canals are also present in the squamous division of the trunk, although there they are known only in a few species in which they are not typically developed. Finally, they were probably present, and in many forms typically developed, in the soft parts of the corium situated between the exoskeletal plates of the electric fields and between the plates of the ventral visceral exoskeleton.

The intra-areal canals, like the inter-areal, are best known in the cephalic shield, but are present throughout the mucous canal system. They are situated in the wide meshes of the plexus formed by the inter-areal canals (*ita, mc,* text-figs. 5–7;

Pl. 4, fig. 3; Pl. 10, figs. 1–3; Pl. 24, figs. 1, 2; Pl. 29, fig. 1; Pl. 32, fig. 4; Pl. 36, fig. 4; Pl. 42, fig. 1; Pl. 44, fig. 1; Pl. 45, figs. 2, 3; Pl. 56, figs. 2, 3; Pl. 57, fig. 3; Pl. 59, fig. 3; Pl. 60, figs. 1–4; Pl. 64, figs. 1–3; Pl. 65, figs. 1–3) and thus in, or superficially to, the polygonal areas of the exoskeleton. They always form with each other a fine-meshed plexus—the intra-areal plexus—and anastomose frequently with the inter-areal canals surrounding their respective polygonal areas. The meshes of the intra-areal plexus vary in shape in the cephalic shield in different forms, whereas in the forms in which they are known in the scales they are there mostly longer than wide (Pl. 65, figs. 2, 3). It is important to note that the intra-areal canals are narrower than the inter-areal canals when the latter are typically developed, but otherwise they may be of about the same width or even wider.

In several forms the arrangement of the inter- and intra-areal mucous canals of the cephalic shield is wholly, or in part, as simple as has been described above, the inter-areal canals being represented only by a single, fairly wide canal between neighbouring polygonal areas, and easily distinguishable from the intra-areal canals. In other forms the inter-areal canals of the cephalic shield are represented by two or more fine canals which frequently anastomose with one another (text-fig. 5C, D; Pl. 45, figs. 2, 3); and in these forms there is sometimes a tendency for the distinction between the inter-areal and intra-areal canals to break down. Finally, in still other forms the inter-areal canals of the cephalic shield may, either throughout their extent or in places, be more or less completely subdivided into a fine-meshed plexus, which in its general characters agrees more or less completely with the intra-areal plexus (text-fig. 5E–G; Pl. 10, fig. 1; Pl. 29, fig. 1; Pl. 32, fig. 4; Pl. 36, fig. 4; Pl. 56, fig. 2; Pl. 57, fig. 3), and thus in these forms it is difficult to distinguish the inter- and intra-areal mucous canals of the cephalic shield from each other: indeed, all these canals may together form a more or less uniform, fine-meshed plexus.

In the few instances in which they are known (Pl. 65, figs. 2, 3) the inter-areal canals of the trunk form a uniformly fine-meshed plexus with the intra-areal canals, from which they cannot be distinguished.

Finally, it should be noted that the mucous canal system has greatly influenced the vascular system of the corium; for, as we have already seen (*cf.* pp. 23–27), all the vascular canals of the corium are arranged in vascular areas, which in shape and extent agree with the polygonal areas of the exoskeleton. It is thus beyond question that it is the mucous canal system which has given the exoskeleton of the Cephalaspids its peculiar structure and appearance of being composed of numerous small polygonal areas. As not only numerous, but also rather wide, vascular canals enter the mucous canal system it is obvious that it was richly supplied with blood.

We thus see that there was a complicated system of anastomosing canals, probably lined by epidermis, situated in the superficial part of the corium, and distributed over the head, the shoulder-girdle, the squamous division of the trunk, and the pectoral fins; that it opened outwards by means of numerous pores, and was richly supplied by blood from the sub-epidermal vascular plexus; and that it greatly influenced the arrangement of the entire vascular system of the corium.

Judging from these facts it seems impossible that the mucous canal system could have had anything to do either with the ampullary organs of the Elasmobranchs (Allis 1901, pp. 90–101, 109–117; Boll 1868, pp. 375–389; 1875, pp. 385–392; Brohmer 1908, pp. 25–40; Johnston 1902, pp. 308–313; Minckert 1901, pp. 497–527; Retzius 1898, pp. 75–82), or with the so-called nerve-sacs of the Acipenserids (*cf.* Merkel 1880, pp. 36–48; Allis 1903, pp. 659–664), which are developed in a very different way and, moreover, are confined principally to the head; and as there is a complete lateral sensory canal system in both the Cephalaspids and Tremataspids, it cannot, of course, represent this system, and we are therefore led to the conclusion that the mucous canal system either was a slime-producing organ or a sense-organ of a special kind, the nature of which cannot be more accurately established.

SYSTEMATIC DESCRIPTION

Family *CEPHALASPIDAE.*

Diagnosis.—*Osteostraci* with cephalic shield well developed and extending more or less far backwards on to the trunk. Pectoral sinuses and pectoral fins always present. Lateral electric field of each side not divided into two but forming a long and uninterrupted organ. Canals of nerves of each lateral electric field not grouped but arranged more or less metamerically, like other nerve and vascular canals.

Remarks.—Of the genera dealt with in this work *Hemicyclaspis*, *Cephalaspis*, *Benneviaspis*, *Securiaspis*, *Thyestes*, *Didymaspis* and *Sclerodus* [*Eukeraspis*] are all referable to the family Cephalaspidae. As for *Ateleaspis*, of which I have examined no material, I am of the opinion that this genus also, at least provisionally, may be included in this family, which would thus at present comprise the following genera: *Hemicyclaspis* Lankester, *Aceraspis* Kiaer, *Micraspis* Kiaer, *Cephalaspis* Agassiz, (?) *Ateleaspis* Traquair, *Benneviaspis* Stensiö, *Securiaspis* Stensiö, *Hoelaspis* Stensiö, *Boreaspis* Stensiö, *Kiaeraspis* Stensiö, *Thyestes* Eichwald, *Didymaspis* Lankester and *Sclerodus* Agassiz.

The family Cephalaspidae is undoubtedly closely related to the family Tremataspidae, but differs clearly from it in certain respects. Thus in the Cephalaspidae there are always more or less distinct pectoral sinuses, which are entirely absent in the Tremataspidae. Further, in the Cephalaspidae each lateral electric field is always long and continuous, but in the Tremataspidae it is divided into two parts which are short and well separated from one another. Finally, in the Cephalaspidae the nerve-canals of the lateral electric field are not specially arranged, whereas in the Tremataspidae they are in two distinct groups, corresponding to the two parts of each lateral electric field. The fact that no member of the family Tremataspidae has pectoral sinuses proves that they lacked pectoral fins.

The family CEPHALASPIDAE thus defined may be divided into two sub-families which I have called CEPHALASPINAE and KIAERASPINAE.

The first of these sub-families, the CEPHALASPINAE, comprises the genera *Hemicyclaspis, Cephalaspis, Aceraspis, Micraspis* and perhaps also *Ateleaspis*. In these the electric fields are always well developed: the dorsal field begins immediately behind the pineal depression and reaches far backwards on to the occipital region, while each of the lateral pair reaches from the rostral part of the cephalic shield backwards on to the cornu of its side or, if cornua are not developed, almost to the pectoral sinus. The lateral field is always without a distinct postero-medial corner in this family, and the canals of its two most anterior nerves are probably always independent of each other as beyond a point close to the side, or just in front, of the orbit, and, moreover, their course is such that the canal of the n. trigeminus proper passes downwards to the oralo-branchial chamber in the space between them. Finally, the canal of the dorso-lateral superficial vein 3 as a rule opens into the postero-lateral corner of the orbit.

The other sub-family, the KIAERASPINAE, comprises the genera *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis, Kiaeraspis, Thyestes, Didymaspis* and *Sclerodus* [*Eukeraspis*]. In this sub-family the electric fields are well developed, except in *Thyestes, Didymaspis* and *Sclerodus*, in which the dorsal electric field always begins somewhat behind the pineal depression and reaches no further back than the most anterior part of the occipital region, approximately as far as the opening of the supposed canal of the ductus endolymphaticus; while the lateral fields have also a more restricted range, both forwards and backwards, than in the other genera, and never continue on to the cornua, even when these are strongly developed. In all the genera of this sub-family, except *Securiaspis* and *Sclerodus*, each lateral electric field has a postero-medial angle, which in *Benneviaspis, Hoelaspis* and *Thyestes* is rather small, but in *Boreaspis, Kiaeraspis* and *Didymaspis* so long that in some instances it completely traverses the zonal part in front of the pectoral sinus. In all the genera of this sub-family also the canals of the two most anterior nerves of the lateral electric field are united with each other for a longer distance forwards than in the sub-family CEPHALASPINAE; in *Boreaspis, Kiaeraspis, Thyestes, Didymaspis* and *Sclerodus* [*Eukeraspis*] they are undivided even as far as the lateral electric field. The canal of the n. trigeminus proper runs down to the oralo-branchial chamber either as in *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis* and *Kiaeraspis*, that is posteriorly to the canal or canals of both the anterior nerves of the lateral electric field, or as in *Thyestes, Didymaspis* and *Sclerodus*, in front of the joint canal of these two nerves. Finally, in this sub-family the canal of the dorso-lateral superficial vein 3 opens as a rule dorsally into the post-orbital division of the canal of the v. capitis lateralis, close behind the orbit.

It should also be mentioned that these two sub-families probably also differ somewhat in certain characters of the squamation and fins. Thus there is, at least in most of the CEPHALASPINAE, either an anterior dorsal fin or a pronounced dorsal crest consisting of a special series of scutes; whereas in certain of the KIAERASPINAE (*e.g. Thyestes*) there are no traces of either such a fin or crest, nor are independent dorso-lateral scales present, these being coalesced with the lateral scales. Among the KIAERASPINAE we have in *Benneviaspis*, *Securiaspis* and *Hoelaspis* genera which in the shape of the cephalic shield, and in the relations of the lateral electric fields and the canals of their two most anterior nerves, form a partial transition to the CEPHALASPINAE.

SUB-FAMILY *CEPHALASPINAE.*

DIAGNOSIS.—CEPHALASPIDAE with electric fields well developed. Lateral electric fields devoid of distinct postero-medial angle. Independent canals of two most anterior nerves of lateral electric field fairly long, their common canal ending just antero-laterally to the orbit. Canal of n. trigeminus proper passing down to oralo-branchial chamber in space between independent canals of two most anterior nerves of lateral electric field. Canal of dorso-lateral superficial vein 3 usually opening into postero-lateral corner of orbit.

GENERA.—*Hemicyclaspis* LANKESTER, *Cephalaspis* AGASSIZ, *Aceraspis* KIAER, *Micraspis* KIAER, and perhaps also *Ateleaspis* TRAQUAIR.

GENUS HEMICYCLASPIS Lankester.

1870. *Hemicyclaspis*, E. R. Lankester, p. 43 (as sub-genus of *Cephalaspis*).

DIAGNOSIS.—CEPHALASPINAE with cephalic shield rather triangular in outline; cornua not developed, and pectoral sinuses therefore ill-defined and without lateral boundaries. Inter-zonal part rather short, its exoskeleton not complete on under-surface of body but represented medially by independent plates. Electric fields well developed, each lateral field ending posteriorly on zonal (shoulder-girdle) part immediately in front of pectoral fin. Canals of two most anterior nerves of lateral electric field united in common canal only as far forwards as antero-lateral corner of orbit. Canal of dorso-lateral superficial vein 3 probably opening into postero-lateral corner of orbit. Middle layer of exoskeleton of cephalic shield with well-developed radiating canals. Trunk triangular in cross-section, except posteriorly in caudal region, where it is narrow and oval. Pectoral fins well developed. Anterior dorsal fin represented only by long dorsal crest consisting of unpaired series of large scutes. Posterior dorsal fin situated far back and provided with strong spine anteriorly. Caudal fin heterocercal but with vestiges of ventral axis supporting special lobe of fin-membrane. Main axis of caudal fin with series of fulcral scales along dorsal margin. Squamation essentially as in *Cephalaspis*, but scales of ventro-lateral ridge (ventro-lateral scales) not extended so as to cover any part of ventral surface of body.

GENOTYPE.—*Cephalaspis murchisoni* Egerton.

REMARKS.—The Cephalaspid remains described by EGERTON in 1857 as *Cephalaspis murchisoni* and *C. ornatus* were in 1870, apparently with good reason, united by LANKESTER in a single species for which he adopted the trivial name "*murchisoni*." Since this species differs from the usual species of *Cephalaspis* in the absence of cornua, LANKESTER established for it a special sub-genus which he named *Hemi-*

cyclaspis. This sub-genus has, however, gained no acceptance until quite recently (Stensiö 1927, p. 246), a circumstance which was certainly due to the fact that its characters have hitherto been so imperfectly known.

Our knowledge of *H. murchisoni* is still imperfect, especially with regard to its anatomy; but it is nevertheless obvious that in most respects it is very like *Cephalaspis*. It differs, however, considerably from *Cephalaspis* in the absence of cornua and consequently in the marked deflection of the posterior part of the lateral electric fields towards the median line. Finally, it also differs from all the other species of which such details are known by the fact that the ventro-median portion of the exoskeleton of the inter-zonal part is represented by independent, scale-like plates, and thus the cephalic shield is not closed ventrally. These differences from *Cephalaspis* seem to me to justify the establishing of an independent genus rather than a sub-genus for this species, though one must remember that it is closely related to *Cephalaspis*. As no prior name is available, the sub-generic name *Hemicyclaspis* must, of course, be adopted as that of the genus.

As far as can be judged from the poorly preserved remains, *Cephalaspis lightbodii* Lankester (1870, p. 55, Pl. 13, fig. 19) also seems to lack cornua and to have the cephalic shield developed very much as in *Hemicyclaspis murchisoni*, and on this account I have placed it provisionally in *Hemicyclaspis*.

1. *Hemicyclaspis murchisoni* (Egerton).

Diagnosis.—A *Hemicyclaspis* with rostral angle fairly obtuse. Cornual angles rather pointed. Exoskeleton with well-developed, continuous superficial layer, with or without tubercular ornament. Mucous canal system enclosed in exoskeleton, either consisting of simple inter-areal canals and network of fine intra-areal canals or developed as more or less uniform, fine-meshed network.

1*a*. *Hemicyclaspis murchisoni* (Egerton), forma typica.

(Text-figs. 5A, 7, 8, 15–17, 18A, 19, 23–26; Pls. 1–7; Pl. 8, figs. 1, 3; Pl. 9; Pl. 10, fig. 2; Pl. 16, fig. 1; Pls. 57, 60; Pl. 64, fig. 1; Pl. 65, figs. 1–3.)

1857. *Cephalaspis murchisonii*, P. M. G. Egerton, p. 284, pl. ix, fig. 1.
1857. *Cephalaspis ornatus*, P. M. G. Egerton, p. 285, pl. ix, figs. 2, 3.
1870. *Hemicyclaspis murchisoni*, E. R. Lankester, p. 51, pl. viii, fig. 6; pl. ix, fig. 1; pl. xii, figs. 3, 4.
1891. *Cephalaspis murchisoni*, A. S. Woodward, p. 185, text-figs. 24, 25; pl. ix, fig. 6; pl. x, figs. 1–4.
1903*a*. *Cephalaspis murchisoni*, W. Patten, p. 847, *etc.*, pl. i, figs. 1, 3, 5; pl. ii, figs. 7, 8.
1911. *Cephalaspis murchisoni*, O. Jaekel, p. 35, text-fig. 21.
1927. *Hemicyclaspis*, E. A. Stensiö, p. 246.

Diagnosis.—Maximum breadth of cephalic shield approximately equalling its length in median line. Dorsal electric field almost twice as long as broad, and broadest slightly in front of middle of its length.

Holotype.—Cephalic shield, in the Museum of Practical Geology, London (No. 8103).

Material.—The material of this species is considerable, consisting of more than seventy specimens, belonging to the following museums: the British Museum (nos. P. 673, P. 676, P. 3238*a*, *b*, P. 3239, P. 5317–P. 5320, P. 6023 (a block with upwards of twelve specimens), P. 6108, P. 6109, P. 6260 with counterpart P. 8804, P. 6261, P. 8800–P. 8803, P. 8803*a*, P. 8805, P. 8806, P. 8807 in counterpart, P. 8808–P. 8825, P. 14010, P. 14012, P. 14013, P. 14016–P. 14018, P. 16151–P. 16153); the Museum of Practical Geology, London (the holotype); the Hereford Museum (four specimens); the Ludlow Museum (one specimen); the Geologisch-Paläontologisches Museum of the University of Berlin (one specimen); the Bay. Sammlung für Paläontologie, etc., Munich (two specimens); the Paleontologisk Museum, Oslo (two specimens) and the Museum of the Geologisch-Palaeontologisches Institut of the University of Tübingen (nos. 1569, 1798). Finally, three of the specimens studied are in the possession of Mr. W. Wickham King, of Hagley. Most of the specimens consist only of more or less imperfect cephalic shields, but there are also several specimens displaying parts of the trunk-skeleton and the fins, especially among the material of the British Museum. One specimen in the British Museum (P. 6023 (I)) is almost complete (Pl. 2, fig. 4; Pl. 3, fig. 4) and gives a good idea of the external shape of the whole animal. On this specimen the restorations shown in text-figs. 15, 23 and 25 have been chiefly based.

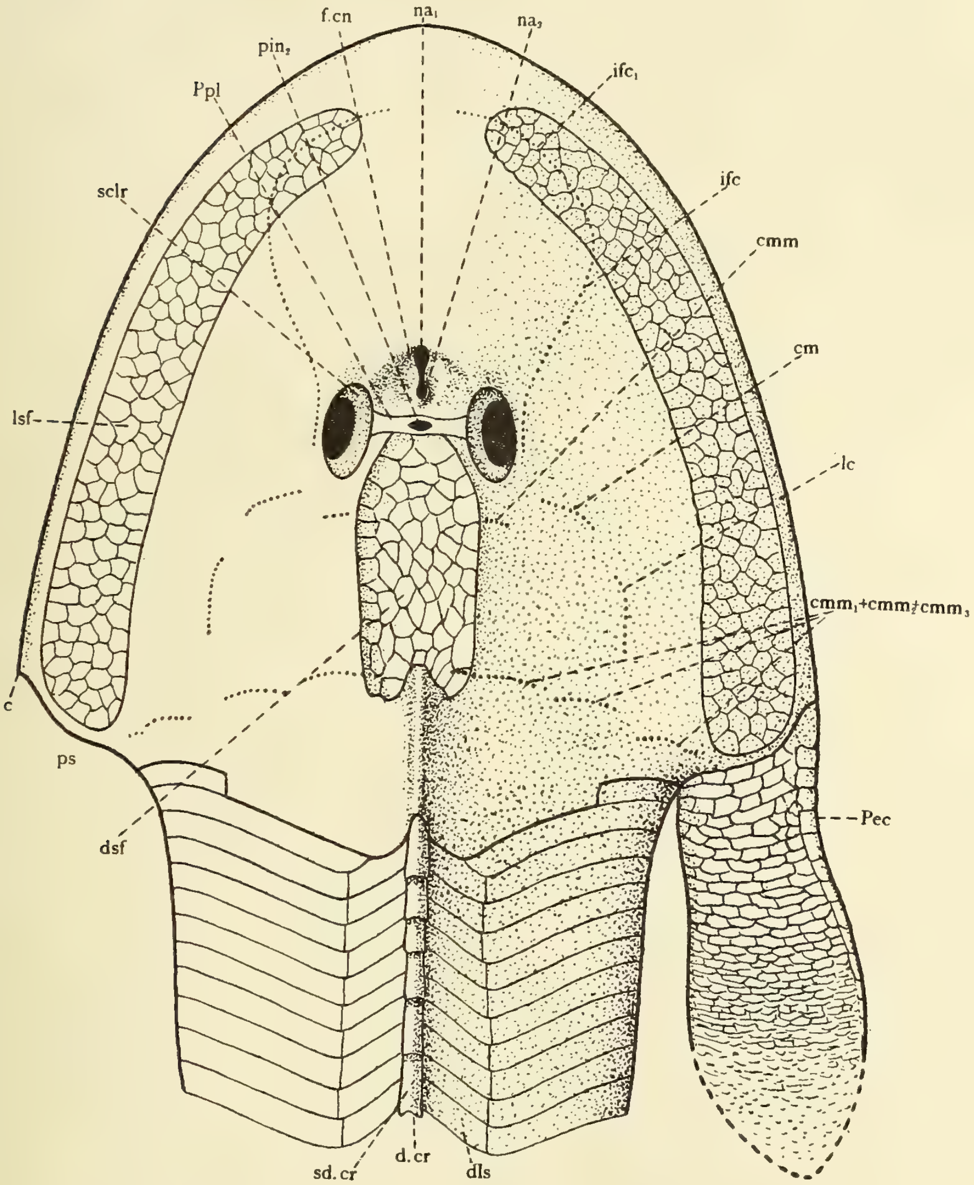
Description.—The species is of moderate size, for the total length does not as a rule exceed 25 cm. and is generally much less, as in the most complete specimen, Brit. Mus. P. 6023 (I), which is 21 cm. long. The length of the cephalic shield constitutes somewhat more than a fourth of the total length of the animal.

The cephalic shield is usually somewhat flattened by pressure and therefore it often appears to be much broader and lower than it actually was in the living animal. Its maximum height, and also its maximum breadth, are far back in the abdominal division. Its length from the anterior end to the posterior angle varies from about 3·5 cm. in the smallest specimens to about 6·5 cm. in the biggest; and, as far as can be judged, the length of the shield was approximately equal to, or only slightly less than, the maximum breadth. Further detailed information concerning the proportions are given in the following table.

Measurements of certain Specimens in the British Museum.

	P. 6023 (I)	P. 14018	P. 6023 (III)	P. 8804	P. 8805	P. 8811	P. 8814	P. 5319
Total length from rostral angle to tip of caudal fin .	about 21 cm.	—	—	—	—	—	—	—
Length of cephalic shield from rostral angle to posterior end of interzonal part . . .	5·4 ,,	3·8 cm.	3·8 cm.	4·5 cm.	6·5 cm.	4·7 cm.	—	about 3·5 cm.
Maximum height of cephalic shield . . .	2·60 ,,	1·3 ,,	1·4 ,,	1·5 ,,	about 3·5 cm.	1·6 ,,	2·4 cm.	—
Maximum breadth of cephalic shield . .	about 5·6 cm.	—		4·4 ,,	7·5 ,,	5·5 ,,	about 6 cm.	—

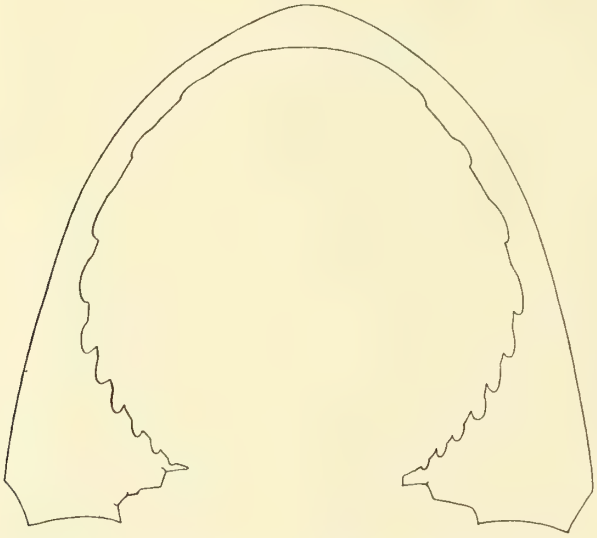
The rostral angle of the cephalic shield is obtuse and rounded. Real cornua are entirely absent, but instead of them a small postero-lateral angle (*c*, text-fig. 23) is present on each zonal part, an angle which, however, does not project laterally



TEXT-FIG. 23.—*Hemicyclaspis murchisoni* (EGERTON). Restoration of cephalic shield, right pectoral fin and anterior portion of squamation of trunk in dorsal aspect, based chiefly on specimen no. P. 6023 (I) in the British Museum. Sensory canals based on several specimens in the British Museum. Approx. × 2 diam.

c, angle corresponding to cornu; *cm*, sensory canal groove perhaps corresponding to the pre-opercular or jugal canal of fishes; *cmm*, sensory canal groove probably corresponding to the middle head-line of pit-organs of fishes; $cmm_1 + cmm_2 + cmm_3$, sensory canal groove (in three pieces) probably corresponding to either the posterior head-line of pit-organs or the supra-temporal cross-commissure of fishes; *d.cr*, dorsal crest; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *f.cn*, circum-nasal fossa; *ifc*, infra-orbital sensory canal groove; ifc_1, anterior division of the infra-orbital groove which probably represents the anterior part of the supra-orbital sensory canal of fishes; *lc*, groove representing anterior part of the cephalic division of the main lateral line of fishes; *lsf*, lateral electric field; na_1, na_2, naso-hypophysial aperture; *Pec*, pectoral fin; pin_2, pineal aperture in pineal plate; *Ppl*, pineal plate; *ps*, pectoral sinus; *sclr*, sclerotic ring; *sd.cr*, scutes of dorsal crest.

beyond the pectoral fin. The pectoral sinus, therefore, has no lateral boundary, and so is ill-defined, especially as its anterior boundary—*i.e.* the posterior surface of the zonal part of the trunk division of the shield—is not concave as in *Cephalaspis* and other forms but, taken as a whole, convex. The inter-zonal part, the breadth of which constitutes more than one-half the maximum breadth of the cephalic shield, is short and its exoskeleton seems to grade into the scales of the trunk. Dorsally, where the inter-zonal part extends furthest backwards, its exoskeleton on each side of the prominent median crest comprises scales belonging at least to one more transverse row than it does lower down : the total number so incorporated seems to be at least four. Ventrally the exoskeleton of the inter-zonal part is incomplete, inasmuch as its right and left halves do not meet in the median line, but are there separated by a wide space occupied by independent plates. These plates are of a type transitional between the ventral trunk-scales and the plates of the ventral visceral exoskeleton. The orbits, which are comparatively small, are situated approximately midway between the rostral angle and the posterior angle. A sclerotic ring (*Sclr*) is present and consists of a continuous circular piece of bone, as in *Saurichthys* (*cf.* Stensiö 1925*b*). The pineal plate (*Ppl*) and its relations are well displayed in several specimens. The dorsal electric field is almost twice as long as broad, and is broadest slightly in front of the middle of its length. Its posterior end is bifurcated so as to embrace the anterior end of the median dorsal crest for a short distance. The pair of lateral electric fields is also well developed, each extending backwards almost to the pectoral sinus. The plates which cover the electric fields are well preserved in several specimens, and it is clear that they consist of the same three layers as the exoskeleton elsewhere on the cephalic shield.



Text-fig. 24.—*Hemicyclaspis murchisoni* (Egerton). Outlines of cephalic shield in ventral aspect. Attempted restoration based on several specimens in the British Museum. Somewhat enlarged.

The endoskeleton of the cephalic shield is always badly preserved. Besides certain perichondrial canal-layers only imperfect remains of the perichondrial bone-layers which lined the oralo-branchial chamber and the labyrinth cavity have been observed so far, a fact which seems to indicate that the degree of ossification was rather slight. The oralo-branchial chamber seems to have been essentially like that in *Cephalaspis*, having similar branchial fossae, inter-branchial ridges and septa (Pl. 6, figs. 1–3; Pl. 7, fig. 5; Pl. 8, fig. 4).[1]

The exoskeleton of the cephalic shield is well developed with a continuous superficial layer (*sl*, Pl. 9; Pl. 57, fig. 2; Pl. 60, figs. 1–4; Pl. 64, fig. 1; Pl. 65, fig. 1). In several of the specimens it is quite smooth, but in others it is ornamented with tubercles or short striae, the detailed arrangement of which, however, is not fully known (Pl. 4, fig. 4).

The mucous canal system of the cephalic shield is well developed and, except most posteriorly where its inter-areal canals are in some specimens represented by more or less open grooves (*iac*, Pl. 9), it is completely enclosed in the exoskeleton. It is of interest to note that it varies considerably in the development of the inter-areal canals, which in some specimens are subdivided into several finer canals, forming with each other a fine-meshed plexus agreeing in all important details so well with that of the intra-areal canals (the intra-areal plexus) that it is difficult to distinguish them (*iac*, Pl. 57, fig. 3); whereas in other specimens they are wide and undivided, at least on the hinder part of the shield, and are thus easily distinguishable from the intra-areal canals which, as usual, form a fine-meshed plexus (*iac*, Pl. 4, fig. 3; Pl. 9; Pl. 10, fig. 2).

The sensory canal system of the cephalic shield is rather well displayed in several specimens, and, as usual, it consists of narrow grooves in the superficial layer. Its distribution is shown in text-figs. 15, 23 and 25.

The visceral exoskeleton consists of small polygonal plates which lie close to one another. These plates probably formed the medial boundary of the external gill-openings and in the neighbourhood of the mouth become somewhat rhombic in shape, at the same time decreasing in size (text-fig. 8). The most anterior plates, which bounded the mouth opening, are not preserved, but as far as can be judged they were mainly as in *Micraspis* (text-fig. 2). All these plates of the ventral visceral exoskeleton are covered by a continuous superficial layer, apparently ornamented like the cephalic shield.

The abdominal region of the trunk is roughly triangular in cross-section (text-figs. 26A–C) and its ventral side is decidedly concave, particularly in front of the anal opening, which is situated approximately between the 36th and 39th transverse rows of scales. The caudal region of the trunk, which is rather long (Pl. 4, fig. 1), gradually decreases in breadth backwards and assumes a narrow, oval shape (text-fig. 26D).

The pectoral fins (*Pec*) are well developed and are covered by imbricating scales which decrease gradually in size distally. On the anterior borders of each of these fins there is a series of distinct marginal scales.

The anterior dorsal fin is reduced to a high dorsal crest (*d.cr*) consisting of a

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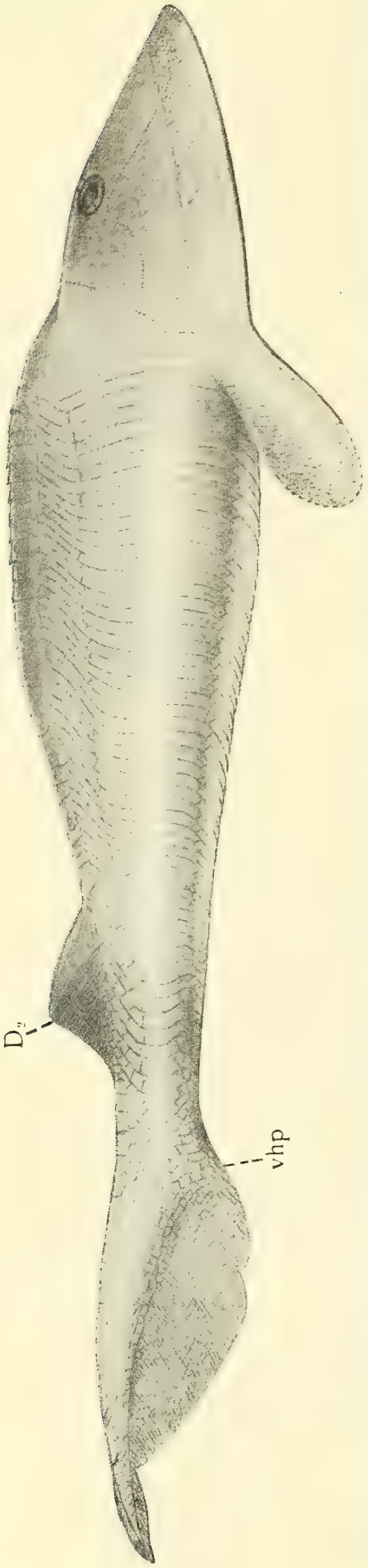
[1] The specimen figured in Pl. 8, fig. 4, is very likely that on which Jaekel, in 1903 in his paper "Über *Tremataspis* und Pattens Ableitung der Wirbeltiere von Arthropoden," based his figs. 3 and 4 of the visceral skeleton.



TEXT-FIG. 25.—*Hemicyclaspis murchisoni* (EGERTON). Restoration of cephalic shield and body in lateral aspect; chiefly after specimen no. P. 6023 (I) in the British Museum. Nat. size. D_2, posterior dorsal fin; *vhp*, ventral axis of the caudal fin, perhaps representing the vestigial axis of an originally hypocercal caudal fin.

series of 12–14 unpaired, imbricating scutes (*sd.cr*). The most posterior of these scutes is several times as long as those preceding it. In addition it is solid in its interior, whereas all the others have an internal cavity which is open basally. This series of scutes reaches from the cephalic shield backwards approximately to the level of the 31st or 32nd transverse rows of trunk-scales.

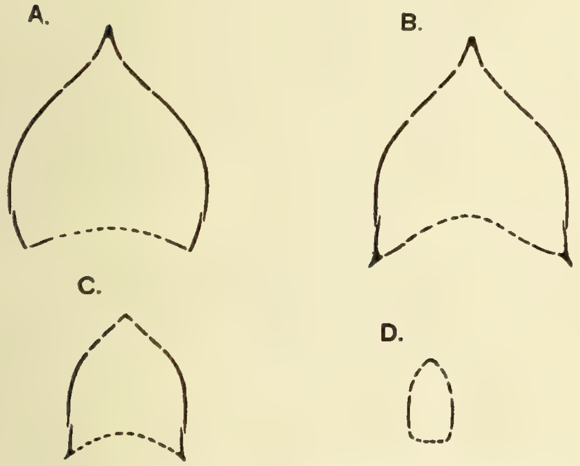
The posterior dorsal fin (D_2), which is fairly small, is situated far back, commencing approximately above the 44th transverse row of trunk-scales or perhaps even a little further backwards. Its anterior border is provided with a strong spine, which, as far as can be seen, consists of a single piece. Behind this spine the fin is covered with small, closely set scales, which are usually arranged in dorso-ventral rows so as to form more or less distinct lepidotrichia.

The caudal fin (*C*) is not well preserved in any of the specimens, but as far as can be made out its shape was as shown in the restorations given in text-figs. 15 and 25. On the whole it is heterocercal in form and the dorsal ridge-scales present along its dorsal margin are to all intents and purposes fulcral scales. It is very remarkable that besides the normal axis the tail has in its anterior ventral part a second, vestigial axis, which will be termed the *ventral axis* (*vhp*). The fin membrane was subdivided into three lobes, a small dorsal lobe situated on both dorsal and ventral sides of the tip of the main dorsal axis of the fin, a large middle lobe on the ventral side of the main axis, and a fairly small and more or less independent ventral lobe supported by the ventral axis of the fin. Like the membrane of the posterior dorsal fin, that of the caudal fin was covered by numerous closely set scales arranged as more or less distinct lepidotrichia.

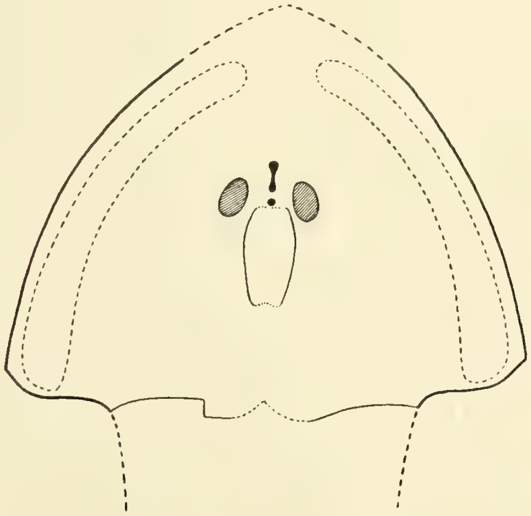
The squamation, which is rather well displayed in several specimens, seems on the whole to resemble that in *Cephalaspis*, but differs in the following respects: the ventro-lateral ridge-scales do not reach so far medially on the ventral surface of the trunk as to cover any part of this surface, and the high lateral scales continue backwards to close in front of the caudal fin. Like the rest of the exoskeleton, the scales are provided with a continuous superficial layer which may be quite smooth or have an ornamentation of tubercles or short striae.

The mucous canal system of the scale-covered division of the trunk and of the pectoral fins is known only in a few specimens, in which it consists of a fine-meshed plexus of canals enclosed in the scales. In this plexus, the meshes of which are longer than high, the inter- and intra-areal canals cannot be distinguished from one another (Pl. 65, figs. 2, 3).

REMARKS.—*H. murchisoni* is characterized by the proportions of the cephalic shield, by the shape and proportions of the dorsal electric field, by the presence of a continuous superficial layer in the exoskeleton and therefore also by the fact that the mucous canal system, except most posteriorly on the cephalic shield in some specimens, is entirely enclosed within the exoskeleton.



TEXT-FIG. 26.—*Hemicyclaspis murchisoni* (EGERTON). Diagrammatic figures showing the outlines of the body in cross-section. A, close behind the cephalic shield; B, somewhat in front of midway between the cephalic shield and the posterior dorsal fin, but still in the region of the dorsal crest; C, somewhat in front of the posterior dorsal fin; D, behind the posterior dorsal fin, in the caudal region.



TEXT-FIG. 27.—*Hemicyclaspis murchisoni* (EGERTON), var. *ludlowensis* nov. Cephalic shield in dorsal view. After the holotype (specimen no. 47806 in the Museum of Practical Geology, London). Nat. size.

At present there is no possibility of distinguishing in this material more than one species. Like LANKESTER in 1870 (p. 51) and A. S. WOODWARD in 1891 (p. 185), I cannot therefore accept the species *C. ornatus* established by EGERTON in 1857 for the specimens that have a tubercular ornamentation.

GEOLOGICAL FORMATIONS AND LOCALITIES.—Downtonian: Ludlow, Shropshire; Ledbury, Herefordshire; Baggeridge Colliery, S. Staffordshire (see also p. 202).

1*b*. *Hemicyclaspis murchisoni* (Egerton), var. *ludlowensis* nov.

(Text-figs. 5G, 27; Pl. 8, fig. 2; Pl. 10, fig. 1; Pl. 11, fig. 1; Pl. 22, fig. 5.)

Diagnosis.—Maximum breadth of the cephalic shield somewhat greater than its length in median line. Dorsal electric field a little less than twice as long as broad.

Holotype.—Cephalic shield in counterpart, in the Museum of Practical Geology, London (nos. 47806–47807), Pl. 10, fig. 1; Pl. 22, fig. 5.

Material.—Beside the holotype, I place in this variety, but with much hesitation, one other specimen, a fragmentary cephalic shield which shows little more than the ventral rim. This is in the possession of the British Museum (no. P. 8829).

Description.—The holotype has the following dimensions: length from the rostral end to the posterior end of the inter-zonal part, somewhat more than 5 cm.; maximum breadth (at the transition between the cephalic and abdominal divisions), about 7 cm.; and maximum height (posteriorly), about 2·5 cm. The other shield—the one in the British Museum—is a little bigger, its length and breadth at the corresponding places being respectively about 6·5 and 9 cm. Both the shields are flattened a little dorso-ventrally and their breadth is therefore somewhat exaggerated, but even if this is taken into consideration it seems likely that they were somewhat broader than those of the typical *H. murchisoni*.

The outlines of the two cephalic shields are very similar to those in the typical form. Certain minor differences are apparent, however, in the configuration of the posterior margin of the zonal part, which is probably also a little broader than in the typical *H. murchisoni*, and the dorsal electric field seems to extend backwards a little less on each side of the median dorsal crest of the inter-zonal part, and is thus perhaps a little shorter in proportion to its breadth.

The perichondrial bone-layers are well preserved in the holotype and appear to be strikingly well developed; and in any case they are much more completely developed than in any of the specimens known so far of the typical *H. murchisoni*. In the British Museum shield, on the contrary, nothing of them was found, probably as a result of its generally imperfect state of preservation.

The exoskeleton, like that of the typical form, has a well-developed, continuous superficial layer. On the dorsal surface of the holotype there is an ornamentation of small, sparsely distributed tubercles of conical shape. On the ventral rim of both shields there are indications of somewhat elongated tubercles or striae which seem to be arranged concentrically with the margin of the rim.

The mucous canal system is in both the shields completely enclosed within the exoskeleton, and forms throughout an almost uniformly fine-meshed network. In fact it is even more difficult to distinguish here between inter-areal and intra-areal mucous canals (Pl. 10, fig. 1) than in those specimens of the typical *H. murchisoni* in which the mucous canal system is similarly developed throughout (Pl. 57, fig. 3).

Remarks.—The two cephalic shields dealt with here agree so closely with *H. murchisoni* that one cannot doubt that they belong to that species. Since, however, they seem to differ from it by a somewhat greater relative breadth, the slightly different shape of the dorsal electric field, and the much less distinct inter-areal canals of the mucous canal system, I have thought it best to describe them as a variety.

The ventral rim figured in Pl. 8, fig. 2, probably belongs either to this variety of *H. murchisoni* or to *H. lightbodii*.

Geological Formation and Localities.—Downtonian: Ludlow, Shropshire; Ledbury, Herefordshire.

2. *Hemicyclaspis lightbodii* (Lankester).

(Text-fig. 28; Pl. 8, fig. 2; Pl. 10, fig. 3; Pl. 11, fig. 2; Pl. 63, figs. 2, 3.)

1870. *Cephalaspis lightbodii*, E. R. Lankester, p. 55, pl. xiii, fig. 19.
1891. *Cephalaspis lightbodii*, A. S. Woodward, p. 190.

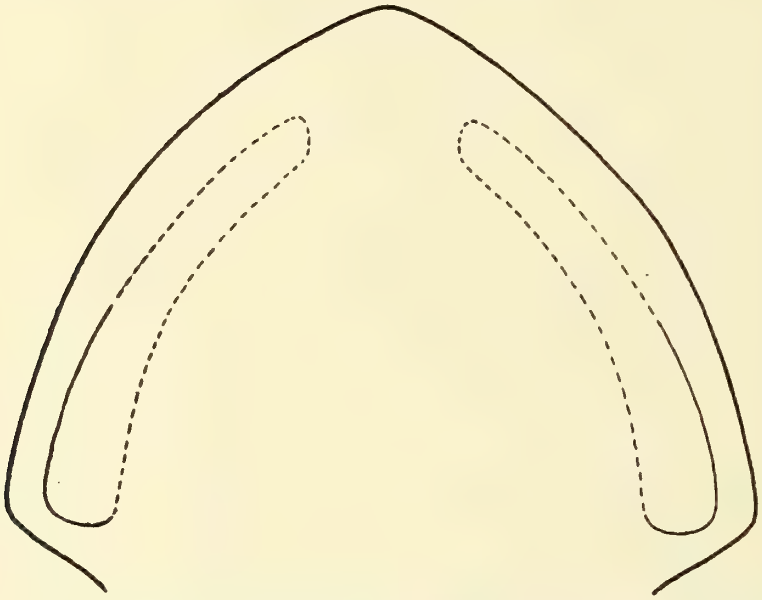
Diagnosis.—A *Hemicyclaspis* with rostral angle distinct; cornual angles rounded off. Dorsal electric field long, about two and a half times as long as broad. Exoskeleton with superficial layer discontinuous; ornamentation consisting of rather coarse tubercles. Mucous canal system represented by open grooves, consisting of wide, well-defined inter-areal grooves and rather few indistinct, anastomosing intra-areal grooves situated between the tubercles forming the ornamentation.

Holotype.—Ventral rim of cephalic shield, in the British Museum (no. 45940).

Material.—The material of this species at my disposal consists of the following specimens: three specimens belonging to the British Museum, the holotype and no. P. 8828, both of which are very imperfect cephalic shields, and no. P. 16154; several specimens belonging to the Museum of Practical Geology, London (nos. 47800–47805), all of which are but fragments of cephalic shields; three specimens belonging to the Ludlow Museum, one of which is the rostral part of a ventral rim, one a dorso-median part of the exoskeleton of a shield with the naso-hypophysial aperture, the orbits and the dorsal electric field, and one a small fragment of a cephalic shield; and finally one specimen belonging to the Hereford Museum, which is also a fragment of a cephalic shield. Thus all the available material of this species is very unsatisfactorily preserved.

Description.—The type-specimen is too imperfectly preserved for exact measurement, but obviously it is from a rather large individual. The other shield belonging to the British Museum (no. P. 8828) is from a somewhat smaller animal. In it the length and maximum breadth—the only measurements which can be made—are as follows: the length from the rostral end to the posterior margin of the inter-zonal part is at least 8 cm.; and the maximum breadth, which like that in *Hemicyclaspis murchisoni* lies approximately at the transition between the cephalic and abdominal divisions of the shield, is about 9 cm., but owing to the much-flattened state of the shield it is very likely that this is somewhat exaggerated, and was thus approximately equal to the length. The other available remains are too imperfect to give any certain idea of the proportions of the cephalic shield.

The rostral margin has a rather pronounced rostral angle. The cornua are entirely absent (text-fig. 28; Pl. 11, fig. 2) and not even the small angles which are found in their place in *Hemicyclaspis murchisoni* seem to be present in this species. The pectoral sinuses are, like those in *H. murchisoni*, not distinctly defined, a condition which is due to the absence of the cornua and to the curvature of the posterior margin of the zonal part. The inter-zonal part is so very imperfectly preserved that little can be said of it, but it seems likely that it was rather broad, and that it had either no dorsal median ridge or but a low ridge at the extreme hinder end. The orbital openings seem to have been fairly small in proportion to the size of the cephalic shield. The dorsal electric field is longer relatively to its breadth than in *H. murchisoni*, its length being almost two and a half times as great as the maximum breadth.



Text-fig. 28.—*Hemicyclaspis lightbodii* (Lankester). Sketch of the general outlines of the cephalic shield. After specimen no. P. 8828 in the British Museum. Nat. size.

The lateral electric fields are well developed and agree completely in their posterior parts with those of *H. murchisoni*.

The endoskeleton of the cephalic shield has not been found preserved in any of the specimens.

The exoskeleton of the cephalic shield differs much from that of *H. murchisoni* in that its superficial layer is present only in the tubercles which form the ornamentation (Pl. 10, fig. 3; Pl. 63, figs. 2, 3). These tubercles, which are confined to the polygonal areas, are present in great numbers and lie fairly close to one another. On the dorsal surface of the shield they are all of an approximately equal height, but elsewhere they vary not a little in their shape: thus they may be either blunt or produced into a more or less well-defined, recurved point; or, when seen from above (or below), they may be either rounded, or angular, or else have the form of short striae. Along the rostral and lateral borders of the shield they are stronger than on the dorsal surface, and several of them there are pointed with apices recurved, so that, as pointed out by Lankester (1870, p. 56), they have a hook-like appearance. Finally, on the ventral rim of the holotype they are of the same type as on the dorsal surface.

The mucous canal system consists of open grooves, which do not represent the inter-areal canals alone, as is usually the case when the superficial layer is present in isolated tubercles only, but also the intra-areal canals (Pl. 10, fig. 3), which evidently lay between the tubercles. Accordingly, we may here distinguish both inter-areal and the intra-areal mucous grooves. As the former are especially wide and distinct, they divide the external parts of the exoskeleton into very conspicuous polygonal areas, which are large in proportion to the size of the cephalic shield.

Remarks.—This species was established on a fragmentary ventral rim by Lankester in 1870 (pp. 55–56), who described it after the other species of *Cephalaspis* with the remark that it was impossible for him to decide to which of the sub-genera of *Cephalaspis* it belonged. From what is now known of it, however, it is obvious that it agrees in so many important characters with *Hemicyclaspis murchisoni* that, at least provisionally, we may be justified in placing it in the genus *Hemicyclaspis*.

H. lightbodii is well distinguished from *H. murchisoni*, especially by the somewhat more pronounced rostral angle of the cephalic shield, by the development of the superficial layer and ornamentation of the exoskeleton of the cephalic shield, and finally by the fact that the mucous canal system of the cephalic shield in the fossil condition is represented throughout by open grooves on the exoskeleton.

Geological Formation and Localities.—Downtonian : Ludlow Shropshire ; Ledbury, Herefordshire.

Genus CEPHALASPIS Agassiz.

1835. *Cephalaspis*, L. Agassiz, p. 135.
1870. *Eucephalaspis*, E. R. Lankester, p. 43 (as sub-genus).
1870. *Zenaspis*, E. R. Lankester, p. 43 (as sub-genus).

Diagnosis.—Cephalaspinae with cephalic shield more or less triangular in general outline and rostral part more or less angular, or rounded, or produced into a rostral process. Cornua usually well developed, directed posteriorly or postero-laterally, not exceeding in length the shield measured in median line, but always extending backwards at least as far as inter-zonal part. Pectoral sinuses well defined. Inter-zonal part complete ventrally. Electric fields well developed, the lateral fields without any distinct postero-medial corner on zonal part in front of pectoral sinus. Canals of two most anterior nerves of lateral electric field united in common canal only as far forwards as orbit. Canal of n. trigeminus proper situated in space between, but at a deeper level than, independent anterior parts of canals of two most anterior nerves of lateral electric field. Canal of dorso-lateral superficial vein 3 opening into postero-dorso-medial corner of orbit. Middle layer of exoskeleton of cephalic shield with well-developed radiating canals. Trunk generally triangular in cross-section. Pectoral fins well developed. Anterior dorsal fin represented only by long dorsal crest, consisting of an unpaired series of large scutes. Posterior dorsal fin situated far backwards with strong anterior spine composed of fulcral scales. Caudal fin heterocercal but with vestiges of ventral axis supporting a partly independent lobe. Squamation consisting of unpaired scutes of dorsal crest and unpaired ridge-scales dorsally, and under these in each transverse row, one or more dorso-lateral scales, one lateral scale, one ventro-lateral scale (in front perhaps two or three) and several ventral scales. Ventro-lateral scale of each row extending medially to cover lateral part of ventral surface of trunk.

GENOTYPE.—*C. lyelli* Agassiz.

REMARKS.—For a detailed account of the history of the genus *Cephalaspis* the reader is referred to my monograph on the Spitsbergen Cephalaspids (1927, pp. 1–2, 246).

In 1870 LANKESTER divided the genus *Cephalaspis* into the three sub-genera, *Hemicyclaspis, Zenaspis* and *Eucephalaspis*. *Hemicyclaspis* was established for the species *C. murchisoni*, *Zenaspis* for the species *C. salweyi*, whereas *Eucephalaspis* was erected for the other species of *Cephalaspis* known at that time. Since the character by which LANKESTER (1870, pp. 43, 55) distinguished *Zenaspis* from *Eucephalaspis* was proved not to exist (WOODWARD 1891, pp. 181, 296) these two sub-genera were not accepted by later writers on *Cephalaspis*, and the sub-genus *Hemicyclaspis* was similarly disregarded. In 1927, however, I found it necessary not only to adopt the latter, but to raise it to the rank of an independent genus (p. 76, and STENSIÖ 1927, p. 246).

The cephalic shield is the only skeletal part usually preserved in species of *Cephalaspis*, and in all of them it appears to be of the same type. The trunk has up to the present time been found in only a few species, but in these its development is essentially uniform, especially in such features as the general shape, the squamation and the number and position of the fins. However, in the new Downtonian material collected by Dr. A. HEINTZ during the Norwegian Spitsbergen expedition in 1928, I have recently found a specimen which has a *Cephalaspis*-like cephalic shield and squamation, but which exhibits distinct traces of a dorsal fin close behind the cephalic shield (D_1, text-fig. 22). Unfortunately, this specimen is rather poorly preserved, so that it is not possible to decide how far this dorsal fin extended backwards, but in any case it is clear from its position that it corresponds to the anterior dorsal fin of *Micraspis* (text-fig. 21). On this account this specimen from Spitsbergen cannot be placed in *Cephalaspis* and a new genus must be erected for it. It is, of course, obvious that for complete generic determination, not only the characters of the cephalic shield of the Cephalaspids but also those of the trunk and the fins must be taken into consideration, and accordingly it is not impossible that the genus *Cephalaspis*, as now defined, will eventually prove not to be a single systematic unit, but to comprise representatives of two or more genera. The genus *Cephalaspis* in its present conception is thus to be considered a provisional genus only.

The characters which are of importance for distinguishing the different species of *Cephalaspis* are as follows :—the general proportions of the animals ; the relation of the length of the cephalic shield to the total length of the animal ; the general shape and proportions of the cephalic shield ; the configuration of the rostral margin of this shield ; the shape, direction and proportions of the cornua ; the presence or absence of denticles on the cornua ; the shape and size of the pectoral sinuses ; the shape and backward extent of the inter-zonal part; the absence or presence and strength of the dorsal ridge or spine on the inter-zonal part, and, if present, its size and position; the size and position of the orbital openings; the shape and extent of the electric fields; the development of the exoskeleton of the cephalic shield, especially that of the superficial layer; the ornamentation of the cephalic shield; the size of the polygonal areas; the development and position of the mucous canal system in, or more or less superficially to, the exoskeleton; the development of the sensory canal system; the development of the squamation and the ornamentation of the scales; and, finally, the development and position of the fins.

The determination of the British species of *Cephalaspis* described below was in some cases very difficult. This was in the first place due to the state of preservation of the material, which is often very poor, but the multiplication of species as a result of the re-examination of the material has made definition difficult, especially when there are two groups of species in which the different forms are very closely allied to each other. One of these groups comprises *C. powriei*, *C. spinifer*, *C. pagei* and *C. watsoni*; the other, *C. lyelli*, *C. lankesteri*, *C. websteri*, *C. fletti*, *C. cradleyensis*, *C. whitbachensis* and *C. whitei*. It should be noted that several of the British species are still so imperfectly known that they must be considered to be only provisional.

In my monograph on the Spitsbergen Cephalaspids no less than nineteen species of *Cephalaspis* were described, all of which were new (Stensiö 1927, pp. 246–288); while among the present material from Great Britain I have distinguished twenty-one species, fourteen of which are new, so that with the four species from Canada[1] the total number of species of *Cephalaspis* described amounts to forty-four. This number will, however, soon be considerably increased, when the description of the new material collected by Heintz in the Spitsbergen Downtonian during the Norwegian Spitsbergen expedition in 1928 is published. Of the forty-four species described hitherto ten are from the Downtonian, but as the new Spitsbergen material just referred to contains a considerable number of undescribed forms, the total number of known species from the Downtonian will soon amount to about twenty.

With a few exceptions the British species of this genus are of a special type characterized by a narrow cephalic shield with small cornua, narrow pectoral sinuses, and a broad and very short inter-zonal part. They resemble most, therefore, the Downtonian species from Spitsbergen, but almost all these have longer and stronger cornua, wider pectoral sinuses and a longer and narrower inter-zonal part. The majority of the species from the Devonian of Spitsbergen, on the contrary, have, like *C. magnifica* from Scotland and *C. jexi*, *C. dawsoni* and *C. laticeps* from Canada, a strikingly broad cephalic shield, long and broad cornua, and in addition often wide pectoral sinuses and a narrow and often fairly long inter-zonal part.

All the British species have a very limited geographical distribution, and none common to Scotland and England has as yet been discovered: in fact, several of them are found only at a single locality or at a few localities situated close together.

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[1] Only four Canadian species have been described hitherto, but it is very likely that the specimen figured by Patten in 1912 (fig. 234, p. 357) represents a fifth species.

Under these circumstances it is, of course, not surprising that I have been unable to discover any species common to Britain and Spitsbergen.

On the basis of the British material studied, the definition which I gave of the genus *Cephalaspis* in 1927 (Stensiö 1927, p. 247) must now be modified in certain details. The new diagnosis is given above (p. 87).

1. *Cephalaspis salweyi* Egerton.

(Text-fig. 29; Pl. 11, figs. 3, 4; Pls. 12, 13; Pl. 25, fig. 1; Pl. 32, fig. 1; Pl. 36, figs. 1, 2; Pl. 58, fig. 3; Pl. 59, figs. 4, 5; Pl. 63, fig. 1; Pl. 66, figs. 1–4.)

1857. *Cephalaspis salweyi*, P. M. G. Egerton, p. 283, pl. x, fig. 1.
1859. *Cephalaspis asterolepis*, R. Harley, p. 503.
1859. *Cephalaspis salweyi*, R. Harley, p. 504.
1869. *Cephalaspis asterolepis*, J. W. Salter, p. 240, and frontispiece.
1870. *Zenaspis salweyi*, E. R. Lankester, p. 52, pl. xii, figs. 2, 5, 6 (*non* pl. viii, figs. 2–4), woodc. figs. 26, 28 (*non* fig. 27).
1881. *Cephalaspis asterolepis*, H. Woodward, p. 193, pl. vi.
1891. *Cephalaspis salweyi*, A. S. Woodward, pp. 181–182 (not specimens nos. 42139, p. 192, 33319).

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured between posterior ends of cornua, generally somewhat exceeding length of cephalic shield in median line. Rostral margin of cephalic shield rounded and usually without distinct rostral angle. Cornua slender, of moderate length, constituting about one-third of distance of their tips from rostral margin of cephalic shield, and without denticles on inner border. Pectoral sinuses rather broad and deep. Interzonal part short, of moderate breadth and with broad, low dorsal spine inclined somewhat backwards. Orbital openings very small. Dorsal electric field about twice as long as broad. Lateral electric fields broad, truncated posteriorly and extending only slightly backwards on to cornua. Exoskeleton with superficial layer discontinuous. Mucous canal system generally situated superficially to, and not enclosed in, exoskeleton; only inter-areal grooves recognizable. Polygonal areas strikingly small in proportion to size of cephalic shield.

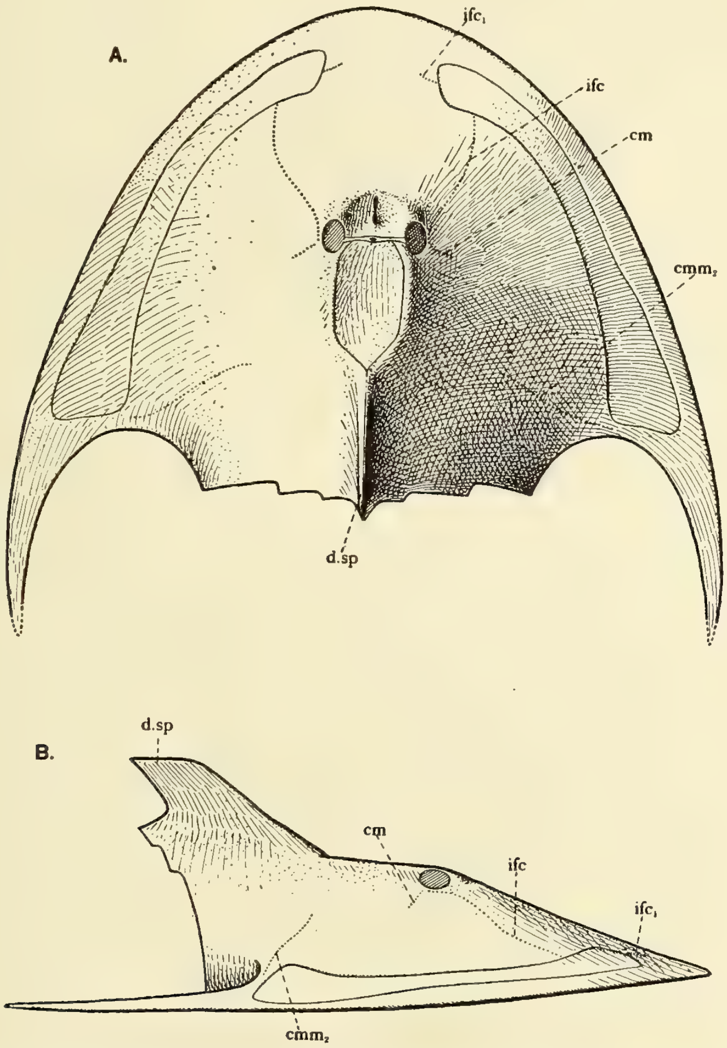
Holotype.—Middle portion of cephalic shield, in Ludlow Museum [H. Salwey Coll.]

Material.—The available material of this species consists of fourteen specimens, ten of which belong to the British Museum (Nos. P. 188 and counterpart P. 190, P. 189, P. 191, P. 5032, P. 5033 in counterpart, 35499, 41186 and counterpart 42131, 42132 in counterpart, 42138, 42144); and four to the Royal Scottish Museum, Edinburgh. All the specimens consist of variously preserved cephalic shields or fragments of such shields. The scale-covered division of the trunk is entirely unknown.

Description.—The largest cephalic shield (Brit. Mus. no. P. 5032) measures approximately 14·5 cm. in length from the rostral margin to the posterior end of the inter-zonal part, while its maximum breadth is about 17 cm. and its maximum height about 6·8 cm. There are among this material, however, remains of cornua which indicate that there were even bigger cephalic shields than this. The smallest cephalic shield known has a length of about 8 cm., while its maximum breadth and height are about 11 and 3 cm. respectively. This species was thus of fairly large size.

With regard to the general proportions of the shield it should be noticed that the maximum breadth always somewhat exceeds the length, and that the breadth of the inter-zonal part constitutes about one-half of the maximum breadth.

The rostral margin as a rule has no rostral angle, such an angle being distinctly developed only in a single specimen (Brit. Mus. no. P. 5032). The cornua, which are directed backwards and somewhat laterally and usually curved slightly inwards, are strikingly slender in proportion to the size of the shield and not especially long. Their length (measured from their tips to the deepest point in the pectoral sinus) is slightly more than one-third of the distance between their tips and the rostral margin of the shield. Their outer and inner margins have no denticles but only tubercles similar to those on the upper and lower sides of the external surface of the shield in general; and there are no pectoral angles. The pectoral sinuses are broad and well



Text-fig. 29.—*Cephalaspis salweyi* Egerton. Cephalic shield. A, dorsal view; B, lateral view. Mainly after specimens nos. P. 188, P. 190, P. 5032 and P. 42132 in the British Museum. Approx. × $\frac{2}{3}$ diam. *d.sp*, dorsal spine. For explanation of other lettering see text-fig. 23.

defined. The inter-zonal part, which is normally the highest part of the shield, is fairly short. It is provided dorsally with a strong spine arising immediately behind the dorsal electric field. The base of the spine continues backwards until somewhat in front of the posterior angle, but not quite to the posterior end of the inter-zonal part, as is generally the case in species of *Cephalaspis*. The orbits, which lie about midway between the rostral angle and the posterior angle, are strikingly small in proportion to the size of the shield, and the pineal plate was probably very narrow. The dorsal electric field is relatively broad and short, its maximum breadth being equal to about one-half, or a little less, of its length. The lateral electric fields extend only very slightly on to the cornua. As is shown by text-fig. 29, both the dorsal and lateral electric fields have a very characteristic shape which makes it fairly easy to recognize even fragments of the shield bearing portions of the electric fields.

The endoskeleton of the cephalic shield is not as a rule preserved. In one specimen, however, remains are found of all of its perichondrial bone-layers (Pl. 25, fig. 1); but it is clear that these layers were very delicately developed and in places probably absent.

The exoskeleton of the cephalic shield is characterized by the presence of the superficial layer and the superficial parts of the middle layer only in the tubercles of the ornamentation. The superficial layer as a rule forms the apical, and the superficial parts of the middle layer the basal, parts of these tubercles, whereas in the spaces between the tubercles the basal parts of the middle layer are exposed in the fossils (Pl. 32, fig. 1; Pl. 58, fig. 3; Pl. 66, fig. 1). The basal layer has its normal structure (Pl. 66, figs. 1, 2) and may in certain specimens exhibit resorption phenomena (Pl. 63, fig. 1; Pl. 66, figs. 3, 4). Partly in and partly beneath the basal layer, and immediately above the sub-aponeurotic (sub-cutaneous) vascular canal plexus there is a system of distinct, ring-shaped grooves, which certainly lodged ring-veins. These ring-veins probably received their blood from the radiating canals and emptied it into the veins of the sub-aponeurotic vascular plexus. The grooves of these ring-veins—the ring-sinuses—are often very conspicuous (*r. sin*, Pl. 11, fig. 4; Pl. 12, fig. 2; Pl. 36, figs. 1, 2; Pl. 59, figs. 4, 5), and are characteristic of the species.

As already mentioned, the ornamentation of the exoskeleton consists of tubercles. On the greater part of the dorsal surface of the shield the tubercles number from two or three to about twelve or fourteen on each polygonal area, but on the ventral rim and on the cornua they are probably present in even greater numbers. Over most of the dorsal surface of the shield and on the ventral rim they are blunt and rounded, but vary much in size, a few on each polygonal area always being much larger than the others (Pl. 11, figs. 3, 4; Pl. 13, figs. 1, 2; Pl. 32, fig. 1; Pl. 58, fig. 3). In front of, and on, the cornua they are often somewhat elongated so as to form short striae, and, in addition, are sometimes pointed with their apices directed posteriorly (Pl. 12, figs. 3, 4; Pl. 13, fig. 1).

The mucous canal system is represented by shallow and rather ill-defined inter-areal grooves only (*iac*, Pl. 32, fig. 1). Of the intra-areal canals there is no trace; but it is nevertheless clear that such canals must have been present, though they must have lain too superficially to the exoskeleton to leave markings on it. The polygonal areas are strikingly small in proportion to the size of the cephalic shield (Pl. 13, fig. 2).

Of the sensory canal grooves those shown in text-fig. 29 could be clearly observed.

REMARKS.—*C. salweyi* is a species which is very well characterized by its large size, the general shape of the cephalic shield, the shape of the electric fields, the development of the superficial layer and the ornamentation of the exoskeleton of the cephalic shield, the presence of very distinct vascular ring-sinuses partly in and partly beneath the exoskeleton of the cephalic shield, the superficial position of the mucous canal system and by the strikingly small size of the polygonal areas of the cephalic shield.

The cephalic shield, no. P. 192 in the British Museum, which was referred to *C. salweyi* by WOODWARD in 1891 (p. 182), differs from this species considerably both in general configuration and ornamentation. As in most of its characters it seems to agree very well with *C. whitei*, I have placed it provisionally in that species.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: Cradley, Herefordshire; Heightington and Acton Beauchamp, Worcestershire; Skirrid Fawr, Monmouthshire.

2. *Cephalaspis whitei*, sp. nov.

(Text-figs. 3B, 9, 30; Pl. 18, figs. 3–6; Pl. 19, figs. 1, 2; Pl. 20, fig. 3; Pl. 21; Pl. 27, fig. 5; Pl. 32, fig. 6; Pls. 61, 62.)

1891. *Cephalaspis lyelli* (in part), A. S. Woodward, pp. 179–181 (nos. 45946*a*, 45947, P. 672, P. 5048; ? no. 37388).
1891. *Cephalaspis salweyi* (in part), A. S. Woodward, pp. 181–182 (? no. P. 192).
1903*a*. *Cephalaspis*, W. Patten, p. 844, pl. i, fig. 4.

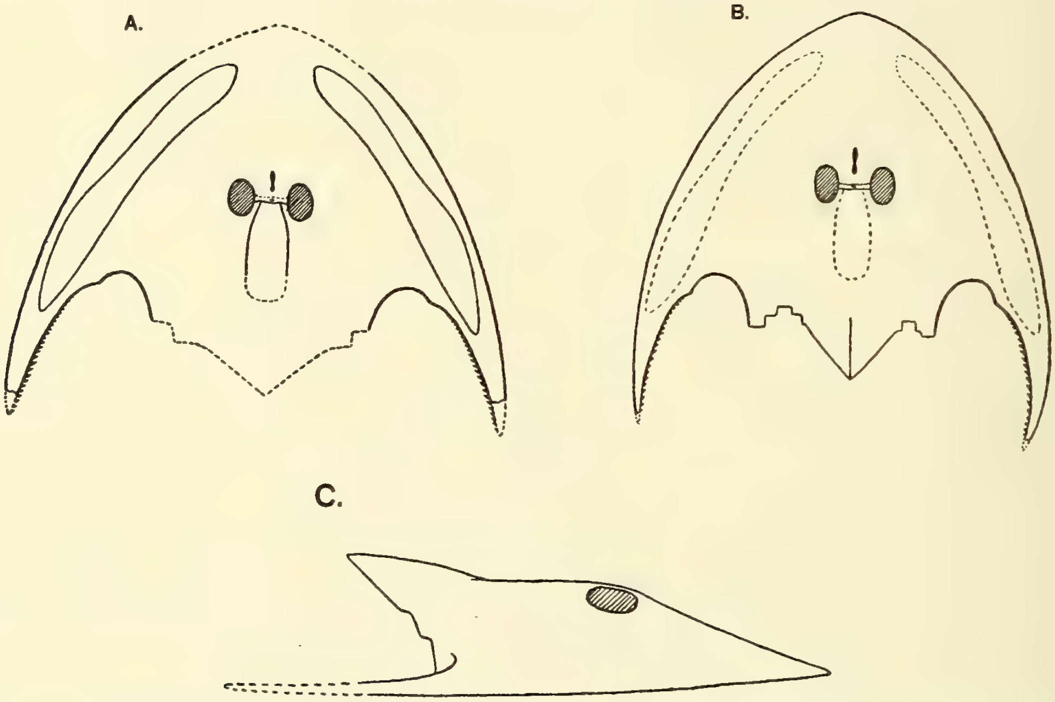
DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across posterior halves of cornua, always somewhat exceeding length of cephalic shield in median line. Rostral angle generally well developed. Cornua projecting in more or less postero-lateral direction, slender and rather long, their length being contained about two and three-quarter times in distance of their tips from rostral angle. Inner border of cornua with forwardly curved denticles. Pectoral angles present. Pectoral sinuses rather deep and narrow. Inter-zonal part of moderate length, rather narrow and with a low, pointed dorsal spine, much inclined backwards. Orbital openings fairly large and situated about middle of length of cephalic shield in median line. Dorsal electric field about two and a half times as long as broad. Lateral electric fields extending somewhat backwards on to cornua and rather pointed posteriorly. Exoskeleton generally with continuous superficial layer and ornamented with numerous small, obtuse tubercles. Mucous canal system usually entirely enclosed in exoskeleton and forming a uniformly fine-meshed network. Polygonal areas fairly large in proportion to size of cephalic shield.

HOLOTYPE.—Cephalic shield, in the British Museum (no. P. 5048), text-fig. 9; Pl. 20, fig. 3; Pl. 21; Pl. 32, fig. 6.

MATERIAL.—The available material which may be safely referred to this species consists only of cephalic shields in various states of preservation. Of these there are no less than twenty-one specimens: eight belong to the British Museum (the holotype and nos. 45946*a*, 45947 in counterpart, P. 672, P. 7167 in counterpart, P. 7168*a*,

P. 8915 and P. 16156); four to the Museum of Practical Geology, London (nos. 6443 and counterpart 6472, 6471 and two counterparts 47794–47795, 47793 and 47808); two to the Sedgwick Museum, Cambridge (nos. A. 3314, A. 3327); two to the University Museum, Oxford (not numbered); one to the Hereford Museum (not numbered); three to the University Museum, Birmingham (not numbered); and one to the Ludlow Museum (not numbered). Besides these shields three additional specimens belonging to the British Museum may with some doubt be placed in this species (nos. 37388, P. 192 and P. 9765).

Description.—The holotype, which is of medium size for the species, measures about 5 cm. in length from the rostral angle to the posterior margin of the inter-zonal part, and its maximum height is about 1·2 cm. or slightly more. Its maximum breadth, measured across the posterior parts of the cornua, may be estimated at about 7·8 cm. and the inter-zonal part is 3·5 cm. broad posteriorly. The distance of the posterior end of each cornu from the rostral angle cannot be directly measured, but is about 7·5 cm.



Text-fig. 30.—*Cephalaspis whitei*, sp. nov. A, B, cephalic shields in dorsal view; C, cephalic shield in lateral view. A, chiefly after the holotype, specimen no. P. 5048 in the British Museum; B, after specimen no. 6443 and its counterpart no. 6472 in the Museum of Practical Geology, London; C, after specimen no. 6471 in the Museum of Practical Geology, London. Nat. size.

The length of the cephalic shield from the rostral margin to the posterior end of the inter-zonal part in the largest specimens is about 6·5 or 7 cm., while in the smallest specimens it amounts only to about 4·5 cm. Thus the species was of medium size.

A more or less obtuse rostral angle is present, at least in some specimens. The cornua, which project in a posterior and usually in a somewhat lateral direction, are long, slender and often slightly curved inwards. Their length is contained about two and three-quarter times in the distance from their tips to the rostral angle. They are characteristically provided on the inner side with numerous but not very long denticles, which are curved slightly forwards; while several specimens have small though distinct pectoral angles. The pectoral sinuses are well defined and fairly deep. The inter-zonal part is of moderate length, about the same as in *C. lyelli*, and dorsally it has a median ridge rising posteriorly to form a dorsal spine, which, however, is very low and inconspicuous. The orbital openings are rather large and lie about midway between the rostral margin and the posterior end of the inter-zonal part. The dorsal electric field is about two and a half times as long as broad. The lateral electric fields run for a short distance on to the proximal part of the cornua and are usually broader in the posterior than in the anterior half.

The endoskeleton is imperfectly known. Remains are found, however, of the external and orbital perichondrial bone-layers and of the perichondrial bone-layers lining the canals of the nerves of the lateral electric fields and also the canals of the sub-aponeurotic (sub-cutaneous) vascular plexus, and in the latter they are in some specimens in a very good state of preservation (text-fig. 9; Pl. 18, figs. 5, 6; Pl. 19, figs. 1, 2; Pl. 20, fig. 3; Pl. 21; Pls. 61, 62).

The exoskeleton seems to be covered by a continuous superficial layer. Its ornament consists of numerous small, usually fairly obtuse tubercles. In some specimens, as for instance in the holotype, the central tubercle of each polygonal area is somewhat larger than the others, while in other specimens all are of fairly equal size. On the upper side of the cephalic division proper the tubercles are rounded, whereas on both the dorsal and ventral surfaces of the cornua and along the lateral margins of the ventral rim they may be slightly elongated (Pl. 32, fig. 6).

The mucous canal system is entirely enclosed in the exoskeleton. It is imperfectly known, but as far as can be judged it consists throughout of a very fine-meshed plexus in which it is impossible to distinguish the inter-areal from the intra-areal canals. The polygonal areas, which, of course, are not visible unless the superficial layer has been destroyed, are comparatively large in proportion to the size of the cephalic shield.

Remarks.—This species has been named in honour of Dr. Errol I. White, of the British Museum (Natural History). It differs from *C. lyelli*, with which it has been confused by previous authors, by the general outlines of its cephalic shield, by the greater length, more slender shape and the usually somewhat more lateral direction of the cornua, by the shape of the electric fields and perhaps also by the ornamentation. Still more than *C. lyelli* it resembles *C. spitsbergensis*, to which it seems to be somewhat closely allied. From this, however, it is distinguished by the rather different shape of the cephalic shield, by the shorter and somewhat more robust cornua, by the presence of denticles on the inner margins of the cornua and by the more posterior position of the orbital openings. There is thus no doubt that it is a distinct species.

The specimens referred with hesitation to this species are all too imperfect to be determined with certainty, but as far as they are known they seem to agree most closely with *C. whitei*.

It should be noted that the holotype is included in Woodward's Catalogue (Part II, 1891, p. 181) under *C. lyelli*, while one of the other British Museum specimens which I place here with some hesitation is in the same work (no. P. 192, p. 182) referred to *C. salweyi*.

Geological Formation and Localities.—Lower Old Red Sandstone: Whitbach and Downton Hall, Shropshire; Whyle Rock, Pontrilas (near) and probably other localities in Herefordshire; (?) Heightington, Worcestershire.

3. *Cephalaspis heightingtonensis*, sp. nov.

(Text-fig. 31; Pl. 14, figs. 5–7.)

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across middle of cornua, exceeding somewhat length of cephalic shield in median line. Anterior end of cephalic shield rather broad but with fairly distinct rostral angle. Cornua projecting straight backwards, of moderate length, this being contained about three times in distance of their tips from rostral angle. Inner margins of cornua with forwardly curved denticles. Pectoral sinuses fairly narrow. Inter-zonal part short and broad; dorsal spine probably absent. Orbital openings probably rather large. Dorsal electric field about two and a half times as long as broad. Lateral electric fields extending backwards on to cornua and pointed posteriorly. Exoskeleton with continuous superficial layer. Mucous canal system enclosed in exoskeleton and forming fairly uniform network.

Holotype.—Cephalic shield in counterpart, in the British Museum (no. 38033, Pl. 14, figs. 5, 6).

Material.—The available material of this species is very limited, consisting only of three cephalic shields, two of which are in counterpart. All belong to the British Museum (the holotype and no. 42142 in counterpart; P. 8830).

Description.—The most completely preserved shield (no. 38033), the holotype, measures in length 1·8 cm. from the rostral angle to the posterior margin of the inter-zonal part, and has a maximum breadth across the middle of the cornua of about 2·5 cm. Its maximum height is about 0·5 cm. or perhaps slightly more, and the breadth of the inter-zonal part most posteriorly about 1·5 cm. Finally, the distance from the posterior end of each cornu to the rostral angle is about 2·5 cm. The other shields are of similar dimensions to the holotype and thus as far as can be judged from this material the species seems to have attained only a small size.

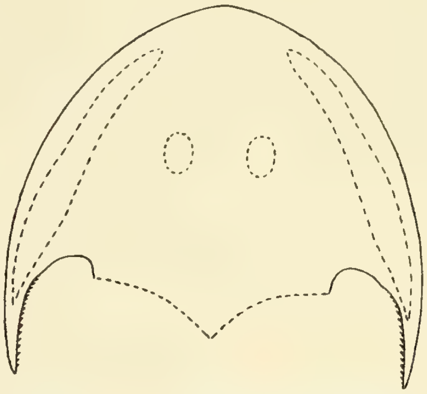
The shield is broad and therefore the rostral angle, though present, is rather indistinct. The cornua, which are directed almost straight backwards, are about 0·85 cm. long and so their length constitutes about one-third of the distance from their tips to the rostral angle. Their inner margins are armed with small denticles which are curved forwards. The pectoral angles are absent. The pectoral sinuses are well defined but rather narrow in proportion to the breadth of the shield. The inter-zonal part, which is fairly short, is posteriorly rather more than half as broad as the maximum breadth. The postero-dorsal portion of the inter-zonal part is only well preserved close behind the dorsal electric field, where there are no indications of a median dorsal crest; nor, so far as can be judged, was there a dorsal spine. The orbital openings are rather large and seem to have been situated either midway between the posterior margin of the inter-zonal part and the rostral angle or slightly nearer the latter. The dorsal electric field is about two and a half times as long as broad. The lateral electric fields extend rather far back on to the cornua, almost to the middle of their length.

The endoskeleton is imperfectly known. It may be mentioned, however, that the orbital bone-layer and the anterior part of the bone-layer lining the oralo-branchial chamber are to be seen.

The exoskeleton is in a poor state of preservation, so that little can be found out about it, but it seems very likely that it had a continuous superficial layer and was without strong ornamentation.

The mucous canal system seems to be entirely enclosed in the exoskeleton. It is very likely that it consisted throughout its extent of a fine-meshed plexus in which inter-areal and intra-areal canals could not be distinguished from one another.

REMARKS.—*C. heightingtonensis* is very suggestive of *C. langi*, which is described in detail below. It differs, however, clearly from this by its smaller size, by its longer and much narrower cephalic shield, by the presence of a definite rostral angle and by the more curved cornua directed straight backwards. It resembles also to a certain extent *C. whitei*, *C. lyelli*, *C. fletti*, *C. whitbachensis*, *C. hoeli* and *C. heintzi*, but is nevertheless easily distinguished from all these species.



TEXT-FIG. 31.—*Cephalaspis heightingtonensis*, sp. nov. Cephalic shield in dorsal view. Mainly after the holotype, specimen no. 38033 in the British Museum. × 2 diam.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Heightington, Worcestershire.

4. *Cephalaspis acutirostris*, sp. nov.

(Text-fig. 32; Pl. 40, fig. 3.)

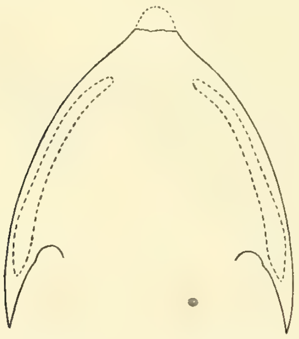
1861. *Cephalaspis lyettii*, S. J. Mackie, text-fig. p. 141.
1870. *Eucephalaspis agassizi* (in part), E. R. Lankester, p. 47, pl. viii, fig. 5.

DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across distal ends of cornua, approximately equal to length of cephalic shield in median line. Anterior end of cephalic shield produced into pronounced rostral process. Cornua projecting directly backwards, rather slender and short, their length about equal to only one-fourth of distance of their tips from end of rostral process (as preserved). Inner border of cornua with pectoral angle, but without distinct denticles. Pectoral sinuses very narrow. Inter-zonal part broad. Tubercular ornamentation present along rostral and lateral margins of shield and along outer margins of cornua. Tubercles on lateral borders of cornua somewhat larger than elsewhere.

HOLOTYPE.—Cephalic shield, in the British Museum (no. P. 9763), Pl. 40, fig. 3.

MATERIAL.—The species is represented only by the holotype. This specimen displays not only the cephalic shield but also a part of the trunk. Unfortunately, however, it is in such a poor state of preservation that only a few of its details can be made out.

Description.—Since the posterior part of the trunk with the caudal fin is wanting the total length of the specimen cannot be exactly ascertained, but it is likely that this did not exceed 11 cm. The maximum height of the trunk is 1·2 cm. or slightly more. The cephalic shield, which is accessible for investigation only from the ventral side, has become somewhat flattened dorso-ventrally and it is therefore not only lower but also probably somewhat broader than in its original condition. As the posterior portion of the inter-zonal part is concealed by the trunk, the length of the cephalic shield from the rostral margin to the posterior margin of the inter-zonal part cannot be given exactly, but it seems that it was between 3·5 and 4 cm. The maximum breadth, which is measured across the posterior parts of the cornua, amounts to about 4 cm., but, as already pointed out, it was probably originally somewhat less. In any case, however, it is evident that it almost equalled the length of the shield from the rostral angle to the posterior margin of the inter-zonal part. The maximum height cannot be ascertained, but it must, of course, have been almost equal to that of the trunk, *i.e.* about 1·2 cm. The inter-zonal part is about 1·7 cm. broad, and the distance from the posterior end of each cornu to the rostral angle about 4·7 cm. The specimen was, therefore, of fairly small size.



Text-fig. 32.—*Cephalaspis acutirostris*, sp. nov. Outlines of cephalic shield. After the holotype, specimen no. P. 9763 in the British Museum. Nat. size.

In general shape the cephalic shield is strikingly narrow in proportion to the length. The rostral part is produced into a broad, but probably short, rostral process, which is, however, imperfectly preserved anteriorly. The cornua, which are directed more or less straight backwards, are rather short and slender, their length constituting only a fourth of the distance from their posterior ends to the anterior end of the rostral process as preserved.

A distinct pectoral angle is present on the inner margin of each cornu, but denticles seem to have been absent there. Along their lateral margins the cornua are provided with obtuse tubercles which are fairly robust, especially posteriorly. These tubercles form the posterior continuation of a series which is present all along the rostral and lateral margins of the shield. The pectoral sinuses are well defined but strikingly narrow. The inter-zonal part is broad, but otherwise its shape and extent are unknown. The orbital openings and the electric fields are not accessible for investigation.

No remains of the endoskeleton have been found. The exoskeleton is in a poor state of preservation, so that it is impossible to decide whether the superficial layer was continuous or not. Except along the rostral and lateral margins the ornamentation is unknown. The mucous canal system is not preserved. The part of the squamation preserved comprises high lateral scales, ventro-lateral scales and very poorly preserved ventral scales. Neither the detailed structure of these scales nor their ornamentation could be investigated.

Remarks.—The specimen here described was assigned by **Lankester** in 1870 to *C. lyelli*. It is, however, evident that it differs from that species by the narrower shape of the cephalic shield, by the distinct though short and broad rostral process and by the much shorter cornua. It is somewhat suggestive of *C. pagei*, but is clearly distinguished therefrom by the rostral process and the shorter cornua. As there is no other form to which it may be referred, I feel justified in establishing a new species for it.

Geological Formation and Locality.—Lower Old Red Sandstone: near Ludlow, Shropshire (see p. 198).

5. *Cephalaspis pagei* Lankester.

(Text-figs. 18B, 33; Pl. 22, fig. 6; Pl. 23, fig. 2; Pl. 32, fig. 5; Pl. 35, fig. 3; Pl. 36, figs. 3–5; Pl. 37, figs. 2, 3; Pls. 38, 39; Pl. 40, fig. 1; Pl. 42; Pl. 43, fig. 1; Pl. 44, fig. 1; Pl. 59, fig. 1.)

1839. *Cephalaspis lyellii* (in part), R. I. Murchison, pp. 588, 590, pl. i, fig. 1.
1870. *Eucephalaspis pagei*, E. R. Lankester, p. 49, pl. x, figs. 3, 4 (*non* pl. xi, fig. 4).
(?)1870. *Eucephalaspis powriei* (in part), E. R. Lankester, p. 48, pl. x, fig. 1.
1891. *Cephalaspis pagei*, A. S. Woodward, p. 183 (not specimens nos. P. 670 and P. 125).
1891. *Cephalaspis powriei* (in part), A. S. Woodward, p. 183 (specimen no. P. 492).

Diagnosis.—A *Cephalaspis* of total length not exceeding 16 cm., but generally less. Cephalic shield constituting rather less than one-third of total length. Maximum breadth of cephalic shield, measured across middle or posterior parts of cornua, exceeding somewhat length of cephalic shield in median line. Anterior end of cephalic shield rather narrow, generally with distinct rostral angle. Cornua projecting backwards and somewhat laterally, fairly broad but only moderately long, their length being contained from three to three and one-third times in distance of their tips from rostral angle; inner border of cornua with rather long, forwardly inclined denticles of uniform type. Pectoral sinuses narrow and rather deep, with fairly distinct antero-medial angle. Inter-zonal part rather long and broad with fairly long dorsal spine much inclined backwards. Orbital openings large, situated somewhat in front of middle of length of cephalic shield in median line. Dorsal part only of sclerotic rings developed. Dorsal electric field about two and a half times as long as broad. Lateral electric fields extending rather far backwards on to cornua and pointed posteriorly. Ventral visceral exoskeleton consisting of numerous small plates. Posterior dorsal fin beginning above the 26–30th transverse rows of scales and with spine consisting of 4–6 pieces. Development of superficial layer of exoskeleton variable. Ornamentation consisting generally of somewhat pointed tubercles which are always a little larger and more obtuse along rostral and lateral margins of cephalic shield and on cornua. Mucous canal system situated either in, or superficially to, exoskeleton, and either comprising distinct intra-areal canals or grooves or forming uniformly fine-meshed network.

Lectotype.—Associated trunk and cephalic shield, in the Royal Scottish Museum, Edinburgh (no. 1891.92.148), Pl. 39, fig. 1; counterpart in the British Museum (no. P. 16148); hereby chosen.

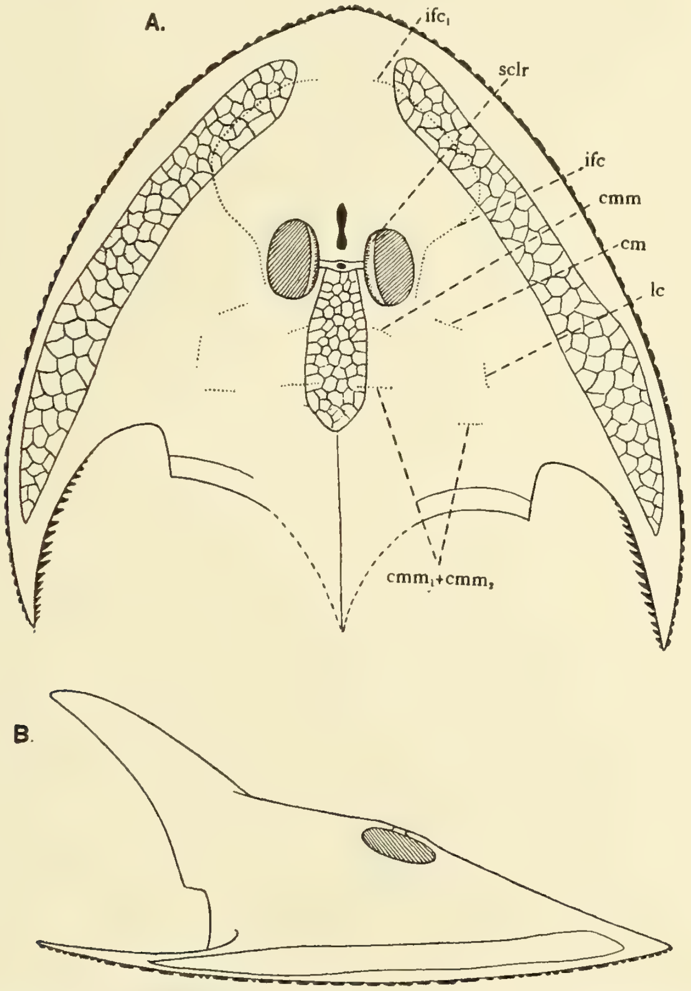
Material.—To this species thirty-one specimens beside the lectotype may be confidently referred. Ten of these belong to the British Museum (nos. 50115, P. 122 in counterpart, P. 123 in counterpart, P. 124, P. 492, P. 6948, P. 6949, P. 6950 in counterpart, P. 6951 and P. 16149); one to the Sedgwick Museum, Cambridge (no. A. 3313); eighteen to the Royal Scottish Museum, Edinburgh (nos. 1891.92.138, 147, 150, 151, 153–161, 168*b*, 171; 1886.31.18; 1887.35; and 1932.17); and two to the Dundee Museum (nos. 3, 9). In addition eleven specimens are placed here with hesitation. Of these one belongs to the British Museum (no. P. 6947); two to the Museum of Practical Geology, London (nos. 47812, 47814); and eight to the Royal Scottish Museum, Edinburgh (nos. 1891.92.139, 141, 143, 152, 181; 1882.16.10; 1895.147.5; and one specimen not numbered). As lectotype I have chosen an Edinburgh specimen (no. 1891.92.148) which was figured by LANKESTER in 1870 (Pl. 10, fig. 4) and was one of the specimens on which he based his original description of the species. The British Museum specimen no. P. 16148 is the counterpart of the lectotype.

Most of the specimens have considerable portions of the trunk associated with the cephalic shield and only relatively few specimens consist of the cephalic shield alone. All the specimens which are embedded in shale are completely flattened dorso-ventrally, whereas those in sandstone are more or less unaffected by pressure.

DESCRIPTION.—The total length of the species from the rostral end to the tip of the caudal fin varies from about 16 cm. in the largest specimens to about 6·5 or 7 cm. in the smallest, but on the average it seems to have been about 9–12 cm.; it was thus a species of fairly small size.

The length of the cephalic shield, measured from the rostral end to the posterior margin of the inter-zonal part, varies from 2 to about 6 cm., according to the size of the specimen, and thus constitutes somewhat less than one-third of the total length of the animal. The maximum breadth of the cephalic shield lies far back, between the lateral margins of the cornua, and measures about 2·8 cm. in the smallest specimens, but reaches about 7 cm. in the largest, although in the unflattened specimens it was somewhat less, and thus about equal to the length. The maximum height of the shield, which as usual is in the posterior half of the inter-zonal part, is certainly rather more than one-third of the length. The distance from the tip of each cornu to the rostral end of the cephalic shield varies from about 2·8 or 3 cm. in the smallest specimens to 6 cm. in the largest.

The cephalic shield is rather narrow anteriorly and has in the typical specimens a more or less distinct rostral angle. The cornua, which project in a posterior and, as a rule, but slightly lateral direction, are somewhat longer than in *C. powriei*, their length being contained about three to three and a third times in the distance from their tips to the rostral angle. They are rather broad, with a pointed posterior end, and have the inner margins provided with fairly long and slender denticles, all of which are of uniform type and distinctly curved forwards. In *C. powriei*, on the contrary, these denticles are usually very broad and obtuse towards the ends of the cornua, and in addition are relatively shorter and less curved forwards. The lateral margins of the cornua are in *C. pagei*, as in *C. powriei*, provided with a series of broad, obtuse tubercles, often somewhat irregular in shape. The pectoral sinuses are well defined but fairly narrow, and their antero-medial corner is, as in *C. powriei*, much more angular than the antero-lateral. The inter-zonal part is broad, its breadth constituting more than one-half the maximum breadth of the shield, and is provided with a dorsal spine which is fairly long but of only moderate height. The orbital openings, which are large in proportion to the size of the cephalic shield and oval in shape, are situated somewhat in front of the middle of the length of the cephalic shield. Remains of the dorsal half of the sclerotic ring with tubercular ornamentation are not infrequently present in the orbital cavities. The dorsal electric field is rather long and narrow, its maximum breadth being contained about two and a half times in its length. The lateral electric fields are well developed and continue backwards as far as middle of the length of the cornua. The exoskeletal plates covering



TEXT-FIG. 33.—*Cephalaspis pagei* LANKESTER. Cephalic shield. A, dorsal view, after specimen no. 1891.92.138 in the Royal Scottish Museum, Edinburgh; B, lateral view, mainly after specimen no. 1895.147.5 in the Royal Scottish Museum, placed with hesitation in this species. × 1½ diam.

For explanation of lettering see text-fig. 23.

the electric fields are preserved in several specimens and resemble those of *Hemicyclaspis murchisoni* (see pp. 47, 80) and the varieties of *C. powriei.*

The perichondrial bone-layers of the endoskeleton of the cephalic shield are imperfectly preserved. Usually only certain canal layers are to be found, but in exceptional cases parts of the orbital and external layers are also to be seen. The canals of the electric nerves of the lateral electric fields are normal for species of *Cephalaspis.*

The exoskeleton of the cephalic shield varies much with regard to the superficial layer. This layer in several specimens forms a continuous covering to the middle layer (Pl. 36, fig. 4); but in others it is present as a continuous covering only in the central parts of each polygonal area, being represented elsewhere only by isolated tubercles (Pl. 42, fig. 1). Finally, in still other specimens it is represented throughout its extent by isolated tubercles only (Pl. 42, fig. 2).

The ornamentation of the cephalic shield is well displayed in several specimens. It consists of tubercles which are somewhat more pointed than is shown in the figure given by LANKESTER (1870, p. 49, fig. 22) and are rounded or slightly elongate in apical view. As a rule these tubercles, though never very large, are well developed, but in certain cases they are very small or almost absent. In the lectotype the tubercles, which are present in fairly large numbers on each polygonal area, are irregularly scattered both on the dorsal and ventral surfaces of the shield, and in addition there are on the central part of each polygonal area, especially on the dorsal surface, one or two tubercles which are somewhat larger and more conspicuous than the others. Several of the specimens agree in their ornamentation with the lectotype, but in others there are no especially large tubercles on the central parts of the polygonal areas; while a few specimens have an ornamentation of numerous tubercles which are more or less distinctly arranged in rows concentric with the borders of each polygonal area. The rostral and lateral margins of the shield, as far back as the posterior ends of the cornua, are in all the specimens provided with one or two series of large, very obtuse tubercles which are somewhat stellate in apical view, agreeing in this respect with those in *C. powriei.*

The mucous canal system of the cephalic shield is entirely enclosed in the exoskeleton where the superficial layer forms a continuous covering to the middle layer, but is represented by open grooves where the superficial layer is present only in isolated tubercles (Pl. 36, fig. 4; Pl. 42). The inter-areal canals or grooves (*iac*) are often of a simple type, so that they are easily distinguishable from the intra-areal canals or grooves; but in many cases they are wholly or partly transformed into a fine-meshed plexus of the same type as the intra-areal plexus. The polygonal areas are large in proportion to the size of the cephalic shield.

The ventral visceral exoskeleton is preserved in a single specimen only. As in *Hemicyclaspis murchisoni,* it consists of numerous polygonal plates with an ornamentation similar to that of the ventral rim of the cephalic shield.

The sensory canal system is displayed in several specimens, and its arrangement is shown in text-fig. 33 (*cf.* also Pl. 36, figs. 3–5; Pl. 40, fig. 1; Pl. 42; Pl. 43, fig. 1).

The trunk is flattened in all the specimens and in such a poor state of preservation that its exact breadth and height cannot be ascertained; but it is evident that it closely resembled that of *H. murchisoni*.

The pectoral fins (*Pec*) are well developed, but they are always imperfectly preserved, so that their exact shape is unknown. As in *H. murchisoni*, they are provided with imbricating scales, which gradually decrease in size distally. No marginal series of scales could be observed. All the scales of these fins are ornamented with tubercles similar to, though much finer than, those on the cephalic shield.

The anterior dorsal fin is represented merely by a high dorsal crest, consisting, as in *H. murchisoni*, of a series of unpaired scutes (*d.cr.*, Pl. 35, fig. 3), of which the exact number cannot be definitely ascertained in any of the specimens.

The posterior dorsal fin lies far back, in the usual way (D_2, Pl. 22, fig. 6; Pl. 35, fig. 5; Pl. 38, figs. 3, 4; Pl. 39, figs. 1, 2). It commences between the levels of the 26th and 30th transverse rows of trunk scales. As in *C. powriei*, its anterior border is provided with a spine consisting of about five pieces which, although they are not coalesced, are nevertheless rigidly connected with one another. The scales covering the fin-membrane are ornamented with small, slightly elongated tubercles. They are, at least to a certain extent, arranged in dorso-ventral rows so as to form primitive lepidotrichia.

The shape of the caudal fin is similar to that of *C. powriei*. The scales covering its membrane are ornamented like those of the posterior dorsal fin (*C*, Pl. 35, fig. 3; Pl. 39, figs. 1, 2; Pl. 40, fig. 1; Pl. 43, fig. 1) and are also arranged in rows so as to form lepidotrichia. In some specimens the ventral axis (*vhp*) of the fin is well displayed. The fulcral scales along the dorsal margin are small.

The squamation of the trunk differs only in certain minor details from that of *Hemicyclaspis murchisoni*. Thus the high lateral scales (*ls*) are in some specimens subdivided into two or more in the region of the posterior dorsal fin (Pl. 22, fig. 6), and it is evident that the ventro-lateral scales are not confined to the lateral surfaces of the trunk and the ventro-lateral ridges only, but extend medially so as to cover also a broad margin on each side of the ventral surface of the trunk (text-fig. 18B, C; Pl. 22, fig. 6; Pl. 39, fig. 1; Pl. 40, fig. 1). The ventro-lateral scales are distinctly highest and have the strongest ventro-lateral processes somewhat in front of the supposed level of the anal opening, *i.e.* where the ventral fin is situated in fishes. In the development of the superficial layer the scales agree in each case with the exoskeleton of the cephalic shield, this layer either forming a continuous covering on the scales or being present only as isolated tubercles.

The ornament on the scales generally consists of numerous, somewhat elongated tubercles and the variation in their development and arrangement corresponds with that of the tubercles on the polygonal areas of the cephalic shield. In a few of the specimens in which the exoskeleton both of the cephalic shield and trunk is provided with a continuous layer the tuberculations may be very fine or even absent.

The mucous canal system of the scale-covered division of the trunk is preserved in only a few specimens, and in these it consists of a fine-meshed plexus with the inter- and intra-areal canals similarly developed.

REMARKS.—*C. pagei* was described by LANKESTER in 1870. Of the three specimens which he then figured two agree closely with each other, but the third—the one figured in his pl. 11, fig. 4—differs so much from the other two that it must certainly represent a distinct species. Such being the case I have retained the specific name *C. pagei* for the two specimens first mentioned, and have established a new species for the third under the name of *C. spinifer* (see below).

C. pagei, as here defined, is in several respects very suggestive of *C. powriei* and its varieties, but is distinguished from these especially by its smaller size, the somewhat different shape of the cephalic shield, somewhat longer cornua, relatively stronger and differently shaped denticles on the inner margins of the cornua, larger orbital openings, a somewhat longer dorsal electric field, a more delicate and differently arranged ornamentation, and by the development of the mucous canals. It also resembles *C. lyelli* and *C. hoeli*, but from these it differs in several characters. It seems, therefore, to be well characterized as a species.

The specimens which I have doubtfully referred to *C. pagei* are all too imperfectly preserved to be determined with certainty. It is probable, however, that most of them do belong to *C. pagei*, but a few may perhaps represent varieties of this species or even represent new species.

Geological Formation and Localities.—Lower Old Red Sandstone: Turin Hill, Tealing, Carmylie, Reswallie and Pitairlie, Forfarshire.

6. *Cephalaspis spinifer*, sp. nov.

(Text-fig. 34; Pl. 46.)

1870. *Eucephalaspis pagei* (in part), E. R. Lankester, p. 49, pl. xi, fig. 4.

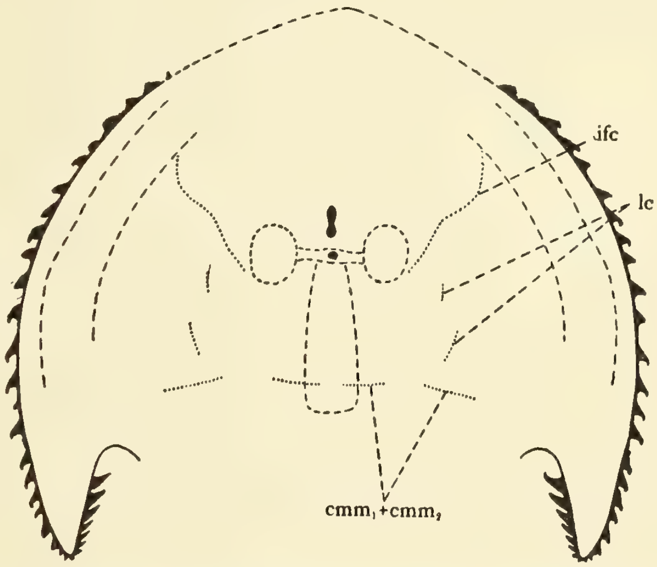
Diagnosis.—A *Cephalaspis* with cephalic shield constituting about one-third of total length. Maximum breadth of cephalic shield, measured considerably in front of bases of cornua, exceeding length of cephalic shield in median line. Cornua projecting backwards, broad and short, their length measuring only one-fourth or one-fifth of distance between their tips and rostral margin of cephalic shield; inner borders of cornua with very strong, forwardly curved denticles. Dorsal part of sclerotic ring developed. Exoskeleton with superficial layer discontinuous. Ornamentation of strong, backwardly curved tubercles or spines somewhat enlarged along margins of cephalic shield. Mucous canal system situated superficially to exoskeleton.

Holotype.—Nearly complete specimen, in the Royal Scottish Museum, Edinburgh (no. 1891.92.149), Pl. 46, fig. 1; counterpart in the British Museum (no. P. 16146), Pl. 46, fig. 2.

Material.—This species is represented only by the holotype in counterpart, which is much flattened but is otherwise fairly complete.

Description.—As the posterior part of the caudal fin and the most rostral part of the cephalic shield are wanting, the total length of the specimen cannot be directly measured, but it was about 5·5 cm., of which the cephalic shield, measured from the rostral end to the posterior end of the inter-zonal part, constitutes about one-third, that is, 2 cm. or slightly less. The maximum breadth of the shield, which is strikingly far in front of the cornua, is about 2·1 cm. The distance from the tips of the cornua to the rostral end of the shield may be estimated at 2·2 cm.

The rostral margin of the cephalic shield is so imperfectly preserved that it is impossible to decide whether there was a rostral angle or not. The cornua, which in their present state of preservation project in a posterior and slightly medial direction, are short, their length constituting only one-fourth or one-fifth of the distance from their tips to the rostral end of the shield. Their inner margins are provided with a series of very strong denticles which are curved forwards. A series of similar, but backwardly curved, denticles is present along the whole of the margin of the shield. The pectoral sinuses and the inter-zonal part are both very imperfectly preserved, but one may see that the latter was short and that it had dorsally a median ridge, which perhaps may have formed a low dorsal spine posteriorly. The orbital openings, which are rather large, are situated in front of the middle of the shield. In each of them are remains of a small, tuberculated sclerotic plate, which obviously corresponds only to a small part of the sclerotic ring of *Hemicyclaspis*. Thus, as in *C. pagei* and *C. powriei*, the sclerotic ring in this species was reduced to a small dorsal portion. The dorsal electric field is so affected by pressure that its original shape cannot be made out. The lateral electric fields are normally developed but their extent backwards on to the cornua cannot be seen.



Text-fig. 34.—*Cephalaspis spinifer*, sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. 1891.92.149, in the Royal Scottish Museum, Edinburgh, and its counterpart, specimen no. P. 16146, in the British Museum. × 4 diam.

$cmm_1 + cmm_2$, grooves corresponding either to the posterior head-line of pit-organs or to the supra-temporal commissure of fishes; *ifc*, infra-orbital groove; *lc*, cephalic division of the main lateral line.

The exoskeleton of the cephalic shield is preserved in a manner little suited to detailed study, and it is impossible to be certain of the state of development of its superficial layer, although it seems to have been discontinuous.

The ornamentation on the dorsal surface of the cephalic shield consists of strong, pointed tubercles, which have their apices curved backwards so as to be somewhat hook-shaped. As far as can be seen there is generally only one such tubercle on each polygonal area; but just posteriorly to the orbital opening, on the raised margin of the dorsal electric field where the polygonal areas are somewhat larger than usual, there are a number of tubercles on each area. Along the rostral and lateral margins of the shield there is, as has already been mentioned, a series of very strong, robust, conical denticles which have their apices turned backwards in the same way as the tubercles on the dorsal surface of the shield. This series continues backwards along the lateral margins of the cornua to their very tips. The arrangement of the ornamentation on the ventral rim is entirely unknown. Thus what is known of the ornamentation of this species is very different from that in both *C. pagei* and *C. powriei.*

The mucous canal system of the cephalic shield seems to have been situated mainly superficially to the exoskeleton. In any case there are hardly any traces of it to be seen on the exoskeleton. The polygonal areas are relatively much smaller than in *C. pagei.*

The sensory canal grooves of the cephalic shield are partly well displayed, and those which can be observed are shown both in text-fig. 34 and Pl. 46.

The trunk is much distorted and in addition is in such a poor state of preservation that nothing of importance can be ascertained as to its proportions.

Of the fins only the caudal can be recognized with certainty, but this fin is most imperfect and all that can be said about it is that it probably did not differ in any essential detail from that of *C. pagei* or *C. powriei.*

The squamation is also very imperfectly preserved, but one can see that the scales are ornamented with large, pointed tubercles similar to those on the cephalic shield.

REMARKS.—The specimen described here was figured by LANKESTER in 1870 (Pl. 11, fig. 4) and assigned by him to *C. pagei.* It differs, however, from that species by the shape of the cephalic shield, the shorter and more robust cornua, much stronger denticles on the cornua, a much coarser and differently arranged ornamentation, and by much smaller polygonal areas. As it also is very different from all other species of *Cephalaspis* known hitherto, it is obvious that it represents a new species, which on account of its ornamentation I have named *C. spinifer.*

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Turin Hill, Forfarshire.

7. *Cephalaspis powriei* Lankester.

DIAGNOSIS.—A *Cephalaspis* attaining a total length of 25 cm., of which the cephalic shield forms approximately one-third. Maximum breadth of cephalic shield, measured across bases of cornua, considerably exceeding length of cephalic shield in median line. Rostral angle not developed. Cornua projecting directly backwards, broad and varying from very to moderately short, their length being contained from three to more than four times in the distance of their tips from rostral margin of the cephalic shield; inner margins of cornua denticulated. Pectoral sinuses with distinct antero-medial corners. Dorsal electric field about twice as long as broad. Lateral electric fields rather obtuse posteriorly and not extending far on to cornua. Development of superficial layer of exoskeleton very variable; ornamentation tubercular; denticles along rostral and lateral margins of cephalic shield obtuse and larger than elsewhere. Condition of mucous canal system variable.

7*a*. *Cephalaspis powriei*, Lankester, forma typica.

(Text-figs. 5F, 35; Pl. 25, fig. 3; Pl. 26, fig. 2; Pl. 27, figs. 1, 2; Pl. 32, figs. 2–4; Pl. 41, fig. 2; Pl. 44, figs. 2, 3.)

1835. *Cephalaspis lyelli*, Agassiz (in part), p. 142, pl. 1*b*, fig. 1.
1870. *Eucephalaspis powriei* (in part), E. R. Lankester, p. 47, pl. ix, fig. 5 (*non* pl. x, fig. 1).
1891. *Cephalaspis powriei* (in part), A. S. Woodward, pp. 182–183 (not specimens nos. P. 492 and 50003).

Diagnosis.—Total length only slightly exceeding 20 cm. Cornua fairly broad, but of moderate length, this being contained about three and a half times in distance of their tips from rostral margin of cephalic shield; inner margins with short, straight denticles, broad and obtuse posteriorly, but more conical and pointed anteriorly. Pectoral sinuses shallow and rather narrow. Inter-zonal part generally short and broad. Orbits small, situated slightly in front of middle of length of cephalic shield. Exoskeleton with continuous superficial layer. Mucous canal system enclosed in exoskeleton. Inter-areal canals forming fine-meshed plexus, finer than that of intra-areal canals.

Lectotype.—Cephalic shield, in the Royal Scottish Museum, Edinburgh (no. 1891.92.146), Pl. 27, fig. 1; Pl. 44, figs. 2, 3; counterpart in the British Museum (no. P. 6944); hereby chosen.

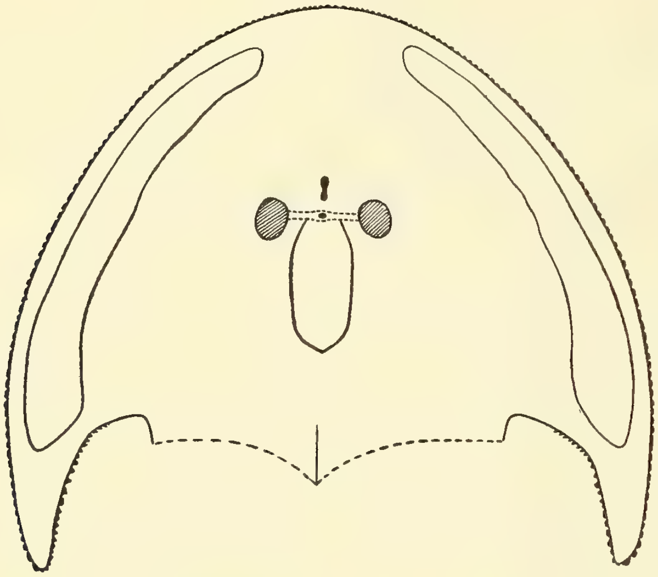
Material.—The material referable with certainty to the typical form of this species consists of the lectotype only. In addition I place here with hesitation two specimens, one of which belongs to the Royal Scottish Museum, Edinburgh (no. 1932.18), and was figured by Agassiz (1835, pl. 1*b*, fig. 1—see Pl. 26, fig. 2, *infra*), and the other to the Bay. Sammlung für Paläontologie, etc., Munich.

The lectotype consists of an isolated cephalic shield. Of the two specimens doubtfully referred to this species, that from Munich consists of a shield with the squamous part of the trunk associated with it, whereas the one belonging to the Royal Scottish Museum, like the lectotype, is represented by an isolated cephalic shield only.

Description.—The species seems to have attained only a moderate size, for the Munich specimen can hardly have exceeded 19 cm. in length from the rostral end of the cephalic shield to the tip of the tail; and the other remains are from individuals scarcely larger.

The cephalic shield probably constitutes about one-third of the total length of the animal. In the lectotype its proportions are as follows:—the length from the rostral margin to the posterior margin of the inter-zonal part cannot be directly measured, since the inter-zonal part is imperfect posteriorly, but it was rather more than 6 cm.; the maximum breadth, which is across the external margins of the anterior parts of the cornua, is 8·4 cm.; and the maximum height, about 1·5 cm. The inter-zonal part is 4·5 cm. broad posteriorly and the distance from the tip of each cornu to the rostral end of the shield, 8·1 cm. The cephalic shield figured by Agassiz seems to be of approximately the same size as, and to have had similar proportions to, the lectotype. Finally, the cephalic shield of the Munich specimen is somewhat smaller than the other two and differs from these also in its proportions, being relatively longer with a longer inter-zonal part.

The rostral margin of the cephalic shield is rounded, without a rostral angle, but nevertheless the rostral part of the shield is not particularly broad. The cornua, which project almost directly backwards and are slightly curved inwards, are rather short and broad, and end posteriorly in a somewhat obtuse point. Their length is contained about three and a half times in the distance of their tips from the rostral margin of the shield. Their inner margins are provided with short, straight denticles, of which the posterior are usually broad and obtuse (Pl. 32, figs. 2, 3), but the anterior are more conical and pointed. The outer margins of the cornua also bear denticles, all of which, however, are broad and obtuse, and form part of the series of enlarged tubercles which is present along the rostral and lateral margins of the shield. The pectoral sinuses are well defined. In the lectotype as well as in the specimen figured by AGASSIZ they are fairly narrow and, as in *C. pagei*, characterized by the fact that their antero-medial corners are angular and much more pronounced than the antero-lateral. In the Munich specimen, on the contrary, the sinuses are rather broad and have no distinctly angular antero-medial corners. The inter-zonal part has dorsally a rather pronounced median crest, which may be produced into a low dorsal spine behind. In the lectotype and in the specimen figured by AGASSIZ this part is short and broad, but in the Munich specimen it is relatively somewhat longer and narrower. The orbital openings are strikingly small and are situated about midway between the rostral margin and the posterior margin of the inter-zonal part. The dorsal electric field is about twice as long as broad. The lateral electric fields, which forwards decrease slightly in breadth, extend only for a short distance on to the cornua. In the Munich specimen the plates covering the electric fields are partly preserved.



TEXT-FIG. 35.—*Cephalaspis powriei* LANKESTER. Cephalic shield in dorsal view. After the lectotype of the *forma typica*, specimen no. 1891.92.146 in the Royal Scottish Museum, Edinburgh. Nat. size.

Of the endoskeleton very little is to be observed in the specimens available. In the lectotype, however, it is clear that the common canal of the two most anterior nerves of the lateral electric field runs further ventro-laterally to the orbit than is normally the case in species of *Cephalaspis*, and consequently does not bifurcate near the antero-lateral corner of the orbit, but at some point distally to it.

The exoskeleton of the cephalic shield is well developed. The basal layer is characterized by the presence in its basal parts of more or less complete ring-sinuses (*r.sin*, Pl. 41, fig. 2; Pl. 44, figs. 2, 3), which are inter-areal in position and thus more or less subdivide the basal layer into polygonal areas. In the lectotype and in the specimen figured by Agassiz the superficial layer forms a continuous covering to the middle layer. The ornamentation of the dorsal and ventral surfaces of the shield consists of tubercles of which the exact shape and arrangement are unknown. The ornamentation of the rostral and lateral margins of the shield as far back as the tips of the cornua consists, as in *C. pagei,* of a series of rather large, very obtuse and somewhat stellate tubercles, which lie fairly close to one another.

The mucous canal system of the cephalic shield in the lectotype and the specimen figured by Agassiz is completely enclosed in the exoskeleton. Its inter-areal canals are subdivided into a fine-meshed plexus which is suggestive of, but nevertheless easily distinguished from, the intra-areal plexus. Its general appearance is well shown in Pl. 32, fig. 4. The polygonal areas are rather small in proportion to the size of the cephalic shield.

The scale-covered division of the trunk is imperfectly preserved, but, as far as can be seen, it seems to have been similar in shape to that of *Hemicyclaspis murchisoni.*

The posterior dorsal fin (D_2) is displayed in the Munich specimen but in a poor state of preservation; despite this it is clear that, as in *Hemicyclaspis murchisoni* and *C. pagei,* it was small and lay far backwards.

The caudal fin (*C*) is also to be seen in the Munich specimen, but is likewise in such a poor state of preservation that it is impossible to determine its exact shape or the arrangement of its squamation, although the latter seems to have been similar to that of *C. pagei.* The ornamentation of the scales is tubercular.

Remarks.—*C. powriei* as here defined is suggestive of *C. pagei,* but differs from this by its larger size, generally different shape of the cephalic shield, shorter and generally more obtuse cornua, shorter, straighter and partly more obtuse denticles on the inner margins of the cornua, smaller orbital openings, a shorter dorsal electric field and by a somewhat differently developed mucous canal system.

Besides the typical form of *C. powriei* there are two other varieties of this species which may be distinguished. These varieties, *C. powriei* var. *brevicornis* and *C. powriei* var. *asper,* are described in detail below.

Geological Formation and Localities.—Lower Old Red Sandstone : Brechin, and probably also Middleton, Forfarshire.

7b. Cephalaspis powriei Lankester, var. *brevicornis* nov.

(Text-figs. 5E, 36; Pl. 22, fig. 7; Pls. 28, 29; Pl. 30, figs. 2, 4; Pl. 33; Pl. 41, fig. 1; Pl. 43, fig. 2; Pl. 58, fig. 2.)

1891. *Cephalaspis powriei* (in part), A. S. Woodward, p. 183 (no. 50003).
1891. *Cephalaspis pagei* (in part), A. S. Woodward, p. 184 (nos. P. 125, P. 670).

Diagnosis.—Total length not exceeding 25 cm. Cornua short, their length only about one-fourth of distance of their tips from rostral end of cephalic shield; inner margins of cornua with short, straight denticles, generally more obtuse posteriorly than anteriorly. Pectoral sinuses shallow and narrow. Inter-zonal part broad, without dorsal spine but with distinct median dorsal crest. Orbits small, situated slightly in front of middle of length of cephalic shield. Posterior dorsal fin with spine consisting of 4–6 pieces. Exoskeleton with discontinuous, rarely continuous, superficial layer. Mucous canal system situated either mainly in, or entirely superficially to, exoskeleton; inter-areal canals forming fine-meshed network, sometimes finer than that of intra-areal canals.

Holotype.—Cephalic shield, in the Museum of Practical Geology, London (no. 47819), Pl. 29, figs. 1–3.

Material.—The material referable to this variety of *C. powriei* consists of eight specimens, of which three belong to the British Museum (nos. P. 125, P. 670, P. 16144); three to the Museum of Practical Geology, London (the holotype and nos. 47785, 47787); and two to the Royal Scottish Museum, Edinburgh (nos. 1895.147.6 and 1891.92.168*a*). In addition to these specimens I place here, though with hesitation, one other belonging to the British Museum (no. 50003) and two in the Royal Scottish Museum (nos. 1891.92.162, 163).

Some of these specimens, like the holotype, consist of isolated cephalic shields only, but others comprise, in addition, the squamation of the trunk. Many of the specimens have been flattened or otherwise distorted by pressure.

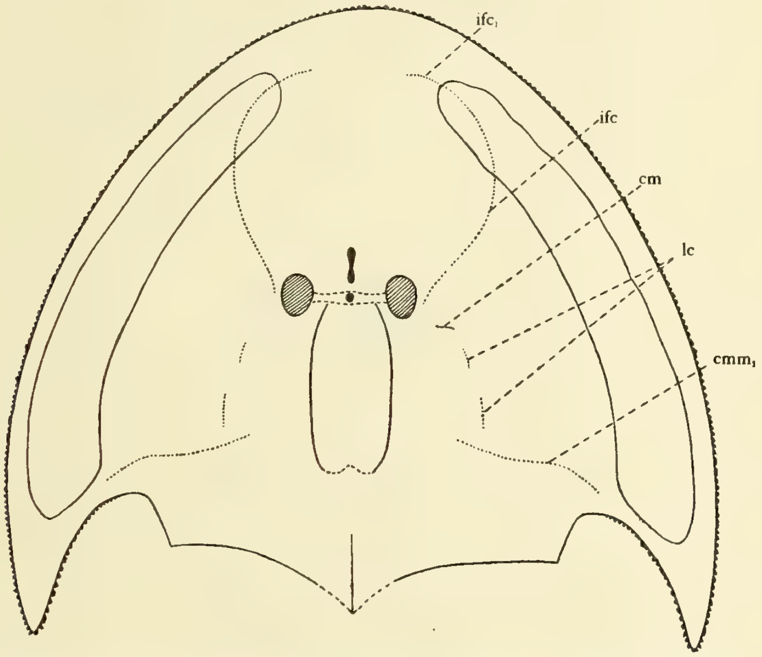
Description.—The total length from the rostral end of the cephalic shield to the tip of the caudal fin is about 16 cm. in the smallest specimens, but although it cannot be directly measured in the largest specimens it seems to have been about 25 cm.

The cephalic shield, from the rostral margin to the posterior end of the inter-zonal part, is between 5·1 and 7·8 cm. long and is thus about one-third of the total length. Its maximum breadth, which in the holotype is at the base of the cornua, but in other specimens further backwards, varies, according to the size of the specimens, from about 7·2 to 11·5 cm., and the distance from the rostral margin of the shield to the tip of each cornu from about 6·7 to 11 cm.

Despite the fact that the rostral margin is destitute of a distinct angle, the anterior part of the cephalic shield is not especially broad, but in many cases even narrower than in the typical form. The cornua, which project directly backwards, are much shorter than in the typical *C. powriei*, their length constituting about one-fourth or even less of the distance from their tips to the rostral margin of the shield. The denticles on the inner margins of the cornua, the pectoral sinuses and also the inter-zonal part are similar to those in the typical form. In the holotype the inter-zonal part has a median dorsal crest but no dorsal spine. The orbital openings are small, as in the typical form, but are situated somewhat nearer the pectoral sinuses. In some specimens there are more or less fragmentary remains of the sclerotic rings. Finally, the electric fields are in all essential details as in the typical *C. powriei*.

The endoskeleton of the cephalic shield in several specimens comprised rather delicately developed perichondrial bone-layers. So far remains of the external, the orbital and the canal layers have been found. The course and place of bifurcation of the common canal of the two most anterior nerves of the lateral electric field are in all respects as in the typical *C. powriei*.

The exoskeleton of the cephalic shield is well developed. The superficial layer may be present as an almost or entirely continuous lining of the middle layer (*e.g.* in the holotype), but in most specimens it seems to occur merely in the tubercles forming the ornamentation. The basal layer is, as in the typical form, characterized by the presence of more or less well developed ring-sinuses (*r.sin*, Pl. 41, fig. 1; Pl. 58, fig. 2), situated entirely within it. The ornamentation consists of tubercles which on the dorsal side of the shield are fairly fine and numerous, but without any definite arrangement and very inconstant in shape, some being more or less pointedly conical and straight, some slightly elongated and curved backwards, and others stellate. Along the rostral and lateral margins of the shield they are enlarged but usually flattened. The exact shape and arrangement of the tubercles on the ventral rim are not known.



TEXT-FIG. 36.—*Cephalaspis powriei* LANKESTER, var. *brevicornis* nov. Cephalic shield in dorsal view, after the holotype, specimen no. 47819 in the Museum of Practical Geology, London. Nat. size. For explanation of lettering see text-fig. 23.

The mucous canal system of the cephalic shield may be situated either entirely within the exoskeleton or entirely outside it. The inter-areal canals or grooves form a fine-meshed plexus which is even finer than the intra-areal plexus, as in the holotype, and therefore easily distinguishable therefrom (text-fig. 5E; Pl. 29, fig. 1), but in other specimens the two are, in places, scarcely distinguishable. In the holotype the polygonal areas are fairly large in proportion to the size of the cephalic shield, but in the other specimens they are generally smaller.

Some of the lateral sensory canal grooves of the cephalic shield are well displayed in the holotype, but only when the exoskeleton is made transparent by means of xylol, so that its interior can be studied.

In general shape the scale-covered division of the trunk probably resembles that of *Hemicyclaspis murchisoni*, *Cephalaspis pagei* and *C. powriei*, forma typica.

The pectoral fins are found in an indifferent state of preservation in several specimens. In that figured in Pl. 43, fig. 2 it is clear that along its margins there are numerous rounded and obtuse tubercles (Pl. 30, fig. 4), but whether these were confined to the margins of the fin or were present also on other parts cannot be decided.

The anterior dorsal fin is probably represented by a series of dorsal scutes, as in *H. murchisoni* and *C. pagei*.

The posterior dorsal fin (D_2) has its usual remote position. It is provided at its anterior border with a spine which, like that in *C. pagei*, is composed of four or five pieces that are fairly rigidly connected. The scales covering the fin-membrane are so imperfectly preserved that nothing of their arrangement can be seen. Both the spine and the scales covering the fin-membrane are ornamented with conical, pointed tubercles which are inclined somewhat backwards, at least on the anterior margin of the spine (Pl. 33).

The caudal fin (C) is well shown in the specimen figured on Pl. 33, where it is clearly seen that it agrees in all essential details with that of *C. pagei* and *H. murchisoni* and that, like them, it has a ventral axis with a partly independent membrane. The scales covering the fin-membrane are very imperfect and their arrangement is accordingly obscure. It seems likely, however, that they were in rows, thus forming primitive lepidotrichia. Their ornament consists of finely pointed, sometimes elongated tubercles.

The squamation, which is fairly complete in some specimens, seems to agree in most respects with that of *C. pagei*, and it is of interest to find that, as in that species, the subdivision of the high lateral scales commences somewhat in front of the second dorsal fin, and that the ventro-lateral scales also extend medially on to the ventral surface of the trunk, so as to cover the marginal areas of this surface. With regard to the structure of the scales it is noticeable that the superficial layer is not continuous in any of the specimens in which the squamation is known. The ornamentation on the scales consists of pointed, often fairly coarse tubercles, which are slightly elongated longitudinally and in many specimens somewhat curved backwards. On the dorsal ridge-scales, the fulcral scales of the caudal fin and the ventro-lateral processes of the ventro-lateral scales, the tubercles appear to be considerably larger than elsewhere.

REMARKS.—This variety seems more closely related to the *forma typica* than is the variety "*asper*," which differs from both the other forms in the width of the pectoral sinuses, the position of the orbits and the shape of the dorsal electric field. *C. powriei* var. *brevicornis* is, however, easily distinguished from the *forma typica*, as its name implies, by the shortness of its cornua and also by the generally discontinuous state of its exoskeleton.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: Turin Hill and Kinblythmont, Forfarshire; Rossie Priory, Perthshire.

7c. *Cephalaspis powriei* Lankester, var. *asper* Lankester.

(Text-figs. 3B, 37; Pl. 26, fig. 1; Pl. 30, figs. 1, 3; Pl. 31; Pl. 58, fig. 1.)

1870. *Eucephalaspis asper*, E. R. Lankester, p. 50, pl. x, fig. 5.
1891. *Cephalaspis pagei* (in part), A. S. Woodward, pp. 183–184 (specimens nos. P. 125 and P. 670).

Diagnosis.—Total length not exceeding 25 cm. Cornua rather broad, robust and long, their length being contained about three times in distance of their tips from rostral end of cephalic shield. Inner margin of cornua with rather small, straight, pointed denticles. Pectoral sinuses probably somewhat wide. Inter-zonal part rather narrow and decreasing rapidly in breadth backwards. Orbits situated slightly behind the middle of length of cephalic shield. Dorsal electric field narrower anteriorly than in other forms of *C. powriei*. Exoskeleton with discontinuous superficial layer. Mucous canal system situated entirely superficially to exoskeleton.

Lectotype.—Specimen lacking tail, in the Royal Scottish Museum, Edinburgh (no. 1891.92.161), Pl. 30, fig. 3; counterpart in the British Museum (no. P. 6946); hereby chosen.

Material.—In addition to the lectotype and its counterpart, a second specimen belonging to the British Museum (no. P. 671) may with a reasonable degree of certainty be placed here. Four other specimens, of which three are in the possession of the Royal Scottish Museum (nos. 1891.92.144, 167, 169) and the fourth in the British Museum (no. P. 16145), are referred with hesitation to this variety.

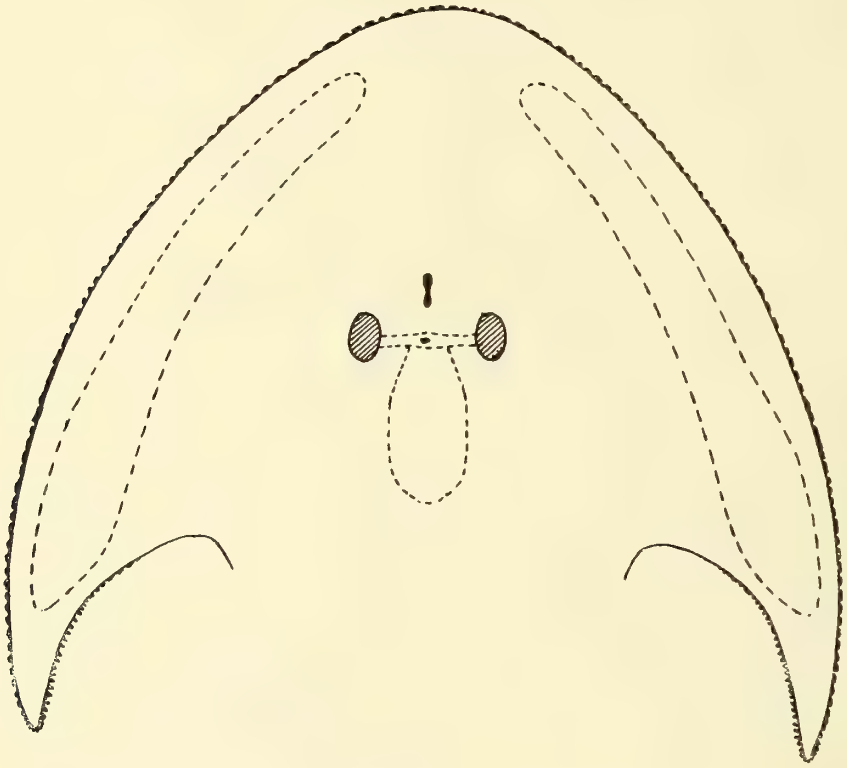
Four of these specimens, among them the lectotype, have considerable parts of the scale-covered division of the trunk preserved in association with the cephalic shield, but the other two consist of cephalic shields only. All are much, some entirely, flattened by pressure.

Description.—In size and general proportions this variety seems to agree with the preceding.

The cephalic shield is from about 6 to 8 cm. long, with a maximum breadth, measured across the anterior or middle regions of the cornua, from about 8 to 11 cm. The distance from the tip of each cornu to the rostral end of the shield is between 7 and 10 cm.

The rostral margin of the cephalic shield is, as in the typical form and the variety *brevicornis*, rounded, without any rostral angle. The rostral part of the shield is fairly narrow, perhaps even narrower than in *C. p. brevicornis*. The cornua, which are broad and robust and project backwards, generally with a slight lateral deflection, are considerably longer than in either the typical *C. powriei* or *C. p. brevicornis*, their length being contained slightly more than three times in the distance from their tips to the rostral margin. Their inner margins are provided with denticles which are stronger and to a certain extent more pointed than in the other forms. On the other hand, these denticles are not nearly as large as in *C. pagei* and differ also in that they are not, or only very slightly, inclined forwards. The lateral margins of the cornua also bear denticles similar to those in the typical form which, like them, form the continuation of the series of enlarged tubercles on the rostral and lateral margins of the shield. The pectoral sinuses in the lectotype and in specimen no.

P. 671 in the British Museum are wider than those in the other forms of *C. powriei*; whereas those in the specimens doubtfully referred to this variety are, generally speaking, similar to them. The inter-zonal part is about as long and broad as in the typical form and *C. p. brevicornis,* except in the lectotype and in specimen no. P. 671 of the British Museum, in which it is somewhat narrower. It has no dorsal spine but only a distinct dorsal crest. The small orbital openings in the two specimens just mentioned are situated further backwards than in either the doubtful specimens or the typical form and the variety *C. p. brevicornis.* While the dorsal electric field is narrower anteriorly and has a more obtuse posterior end and perhaps also a somewhat greater relative maximum breadth, the lateral electric fields agree on the whole with those in the other forms. The exoskeletal plates covering the electric fields are preserved in three of the specimens (the lectotype, specimen no. P. 671 in the British Museum, and no. 1891.92.167 in the Royal Scottish Museum).



TEXT-FIG. 37.—*Cephalaspis powriei* LANKESTER, var. *asper* LANKESTER. Cephalic shield in dorsal view. After the lectotype, specimen no. 1891.92.161 in the Royal Scottish Museum, Edinburgh. Nat. size.

Remains of the endoskeleton of the cephalic shield are found only in specimen no. P. 16145, in which a great many of the canal layers and a part of the external layer are preserved. This external layer shows clearly the posterior extent of the endoskeleton in the dorsal part of the cephalic shield (text-fig. 3B; Pl. 26, fig. 1). The course of the common canal of the two most anterior nerves of the lateral electric fields is similar to that in the main form and the variety *C. p. brevicornis*, and the canal bifurcates at the same point (Pl. 26, fig. 1).

The exoskeleton of the cephalic shield is well developed, but its superficial layer is not continuous in any of the specimens, and whether ring-sinuses are present in the basal layer cannot be decided. In the holotype and in specimen no. P. 671 in the British Museum the ornamentation is so imperfectly preserved that one can only say that it consists of numerous, rather fine and irregularly placed tubercles, which are enlarged and shaped as in the other forms of *C. powriei* along the rostral and lateral margins of the shield. In the four doubtful specimens the ornamentation also consists of numerous, irregularly placed tubercles, which are similarly developed along the margins of the shield. On the dorsal side of the shield, however, they vary in form in different specimens : in some they are conical and fairly straight, but in other specimens they are slightly elongated and more or less ramified or stellate in shape, and their apices are somewhat curved backwards.

The mucous canal system of the cephalic shield lay entirely superficially to the exoskeleton and nothing is therefore definitely known of its development. It is very likely, however, that it did not differ from that in the other forms. The polygonal areas are not especially large.

The sensory canal grooves are fairly well displayed in one of the specimens doubtfully referred to this variety (Pl. 31).

The scale-covered part of the trunk seems to agree in its general shape with that in *C. p. brevicornis.*

The pectoral fins, the posterior dorsal fin and the caudal fin are essentially as in the main form and its other variety. In specimen no. 1891.92.167 in the Royal Scottish Museum at least the scales covering the membrane of the caudal fin are arranged as lepidotrichia.

The squamation is similar to that in *C. p. brevicornis.* The superficial layer of the scales is not continuous, and the ornament on the scales agrees in each specimen generally with that of the cephalic shield.

REMARKS.—The lectotype of this variety and another specimen unfigured were considered by LANKESTER to represent an independent species, *Eucephalaspis asper,* but these were referred by WOODWARD (1891, pp. 183–184) to *C. pagei.* As in its size, the general shape of the cephalic shield, the form of the denticles on the cornua, the small size of the orbits and the shape and proportions of the electric fields this form differs from *C. pagei* and agrees with *C. powriei,* it must be more closely allied to the latter species than to *C. pagei*; but since, however, it differs in some details from both the typical form of *C. powriei* and from *C. powriei* var. *brevicornis* I consider that it represents a distinct variety of *C. powriei,* for which LANKESTER'S trivial name " *asper* " must be retained.

As specimen no. P. 671 in the British Museum agrees in general with the lectotype I have no hesitation in placing it here, but while the other specimens resemble the holotype in several characters fairly well, they differ from it in others, as for instance in the general shape of the cephalic shield. It is therefore not unlikely that these specimens either represent an additional variety of *C. powriei*, or, as in the case of no. P. 16145 in the British Museum, they may belong to *C. watsoni*, which is probably a closely related species.

C. powriei var. *asper* differs from the typical form of *C. powriei* and from *C. powriei* var. *brevicornis* chiefly in the somewhat different general shape of the cephalic shield, longer cornua, somewhat differently shaped denticles on the inner margins of the cornua and by the slightly different shape of the dorsal electric field.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Turin Hill, Forfarshire.

8. *Cephalaspis traquairi*, sp. nov.

(Text-fig. 38; Pl. 23, fig. 3.)

DIAGNOSIS.—Maximum breadth of cephalic shield, measured approximately across bases of cornua, somewhat less than length of cephalic shield in median line. Anterior parts of cephalic shield narrow, but without rostral angle. Cornua projecting posteriorly and slightly laterally, broad and robust, with strongly convex lateral margin; length of cornua contained about three and a half times in distance of their tips from rostral margin of cephalic shield; inner border without denticles. Pectoral sinuses fairly broad and deep. Inter-zonal part of average length decreasing rapidly in breadth towards rear. Orbital openings small, situated somewhat in front of middle of length of cephalic shield in median line. Dorsal electric field about twice as long as broad. Lateral electric fields extending far backwards on to cornua. Exoskeleton with continuous superficial layer, at least along margins of cephalic shield. Ornamentation of small obtuse tubercles along posterior parts of lateral margins of cephalic shield and cornua.

HOLOTYPE.—Cephalic shield in the Royal Scottish Museum, Edinburgh (no. 1902.23), Pl. 23, fig. 3.

MATERIAL.—The material referable to this species consists of the holotype only.

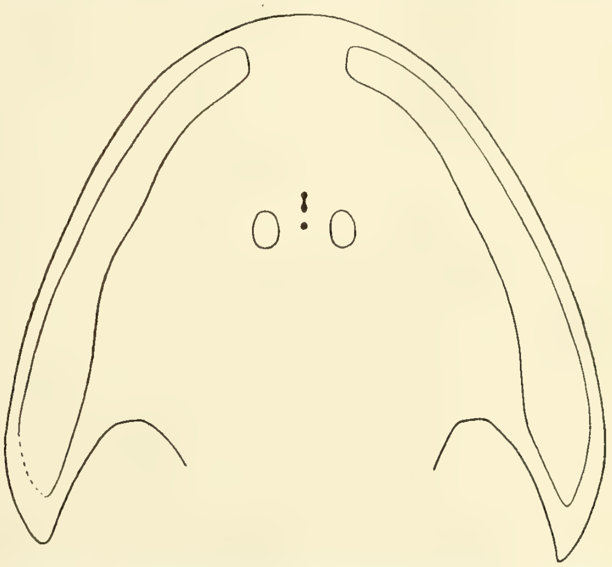
DESCRIPTION.—This cephalic shield lacks a considerable portion of the inter-zonal part posteriorly, and its length from the rostral margin to the posterior margin of the inter-zonal part can therefore only be estimated, about 6·5 cm. The maximum breadth of the shield, which is slightly behind the junction of the cornua and the cephalic division proper of the shield, is 8·1 cm., while the maximum height, situated in the posterior half of the inter-zonal part, is at least 2 cm. The distance from the posterior end of each cornu to the rostral margin of the shield is 8·1 cm., and thus equals the maximum breadth. The shield is therefore of moderate size.

The anterior half of the shield is rather narrow compared with the posterior half, but despite this, the rostral margin is rounded and without a rostral angle. The cornua, which project almost directly backwards, are strikingly broad with very convex outer margins. They are very flat, and their length is contained about three and a half times, or slightly more, in the distance from their tips to the rostral margin of the shield. The pectoral sinuses are well defined and deep but fairly narrow. The inter-zonal part, which is not especially long, decreases rapidly in breadth backwards, so that posteriorly it is strikingly narrow, its breadth there being much less than one-half of the maximum breadth of the shield. On the dorsal side of the inter-zonal part was a median dorsal ridge, but this is very imperfectly preserved and it is impossible to decide whether it continued posteriorly as a ridge or was produced into a dorsal spine. The orbits, which are fairly small in proportion to the size of the cephalic shield, are situated somewhat in front of the middle of the length of the shield. The dorsal electric field is so imperfectly preserved that its exact shape cannot be ascertained, but as far as can be judged it was about twice as long as broad. The lateral electric fields extend very far backwards, over two-thirds of the length of each cornu.

Of the endoskeleton of the cephalic shield only traces of the canals of the nerves of the lateral electric fields are to be observed, but it is obvious that these canals were as normally in *Cephalaspis*.

The exoskeleton of the cephalic shield seems to have been well developed but it is so weathered that it is difficult to be sure of any of the details of its superficial layer. Along the rostral margin and the anterior parts of the lateral margins, however, this layer seems to have been continuous. The ornamentation on the dorsal and ventral surfaces of the shield is unknown, but on the posterior parts of the lateral margins and on the outer borders of the cornua it consists of small, very obtuse and fairly closely set tubercles. The inner margins of the cornua are smooth.

On account of the state of preservation of the exoskeleton nothing is known of the mucous canal system.



Text-fig. 38.—*Cephalaspis traquairi*, sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. 1902.23 in the Royal Scottish Museum, Edinburgh. Nat. size.

Remarks.—*C. traquairi* is well characterized, especially by the general shape of the cephalic shield, the shape and proportions of the cornua and the absence of denticles along their inner borders, the narrowness of the hinder end of the inter-zonal part and by the considerable extension backwards on to the cornua of the lateral electric fields.

In addition to the specimen described here it is possible that a specimen in the palaeontological collection of the University of Glasgow, determined as *C. lyelli*, in fact belongs to *C. traquairi*. This specimen is from the same locality as the holotype and has certain features in common with it; but as I have had the opportunity to study only a cast of it I do not venture to place it definitely in this species.

Geological Formation and Locality.—Lower Old Red Sandstone: Tulloch Quarry, Galston Moor, Ayrshire.

9. *Cephalaspsis lornensis* Traquair.

(Text-fig. 39; Pl. 35, figs. 1, 2.)

1898. *Cephalaspis lornensis*, R. H. Traquair, p. 83.
1899*a*. *Cephalaspis lornensis*, R. H. Traquair, p. 591, with plate.

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across middle or posterior parts of cornua, somewhat less than length of cephalic shield in median line. Rostral angle probably not developed. Cornua projecting directly backwards and very short, their length being contained not less than five times in distance of their distal ends from rostral end of cephalic shield; inner margins of cornua without denticles. Pectoral sinuses narrow. Inter-zonal part broad and rather short. Orbital openings rather large, situated in front of middle of length of cephalic shield. Dorsal electric field somewhat more than twice as long as broad. Exoskeleton with a continuous superficial layer. Ornamentation tubercular. Mucous canal system probably enclosed in exoskeleton.

Lectotype.—Cephalic shield (specimen described and figured by Traquair, 1899*a*, p. 592, Pl. fig. 1), in the collection of the Geological Survey of Scotland, Edinburgh; hereby chosen.

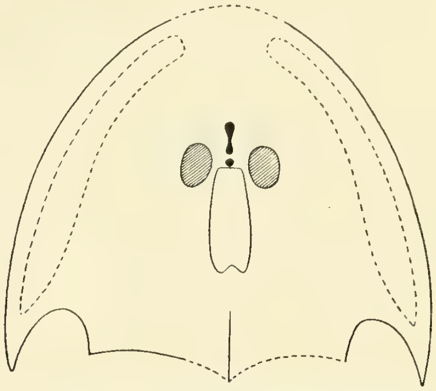
Material.—I have not had the opportunity of examining Traquair's syntypes, but I chose the original of his fig. 1 as lectotype, since it was on that specimen that his description was principally based. The material available to me consists of two imperfect cephalic shields, one of which belongs to the British Museum (no. P. 9642) and the other to the Royal Scottish Museum, Edinburgh (no. 1901.68.27).

Description.—Both the shields are of approximately the same size. In that belonging to the Royal Scottish Museum, which is the better preserved, the dimensions are as follows:—the length from the rostral margin to the posterior margin of the inter-zonal part is about 4 cm.; the maximum breadth, which is situated between the posterior parts of the cornua, cannot be directly ascertained, as the right cornu and certain other parts of the right side are lacking, but it may be estimated to be between 5 and 5·5 cm.; the maximum height, which as usual lies in the inter-zonal part, is very small, as the shield is much flattened dorso-ventrally. Finally, the distance from the posterior end of each cornu to the rostral margin is 5·2 cm.

These two shields are rather small, but as Traquair (1899*a*, p. 593) in his original description mentioned a much larger shield, it seems likely that the species attained a fair size.

In both the shields the rostral margin is imperfectly preserved, but, as far as may be judged, it was destitute of a distinct rostral angle. The cornua, which project in a posterior and very slightly lateral direction, are strikingly short, almost as short as in *Kiaeraspis*, constituting only about a fifth, or even less, of the distance from their tips to the rostral margin. Another very characteristic feature of this species is that the cornua extend only very slightly backwards beyond the inter-zonal part; moreover they are pointed and destitute of real denticles on their inner margins. The pectoral sinuses are well defined but fairly narrow. The inter-zonal part is broad and short, and has dorsally a distinct median crest, but whether this ended in a spine posteriorly, as described by Traquair, it is impossible to discover in the available material. The orbital openings, which are large, are situated in front of the middle of the length of the shield. The dorsal electric field, which is broadest in its posterior half, is somewhat more than twice as long as broad. The lateral electric fields are well developed, but their extent on to the cornua is unknown.

In both cephalic shields there are remains of the perichondrial bone-layers lining the canals of the nerves of the lateral electric fields. In the shield belonging to the Royal Scottish Museum (Pl. 35, fig. 1) we find in addition remains of that part of the external perichondrial bone-layer which lines the occipital region, the posterior surface of the otic region, and the adjacent surface of the endoskeletal shoulder-girdle. In this specimen the posterior boundary of the endoskeleton in the cephalic shield is therefore clearly displayed.



Text-fig. 39.—*Cephalaspis lornensis* Traquair. Cephalic shield in dorsal view. After specimen no. 1901.68.27 in the Royal Scottish Museum, Edinburgh. Nat. size.

The exoskeleton of the shield is imperfectly preserved, but it is obvious that it was well developed. As far as can be seen its superficial layer is continuous. The ornamentation consists of numerous fine, flat tubercles on the ventral rim and on the ventral surface of the cornua, and it is probable that it was similar on the dorsal side of the shield.

The mucous canal system cannot be observed, but it seems most probable that it consisted of fine canals enclosed in the exoskeleton.

Remarks.—*C. lornensis* is easily distinguished from other species of *Cephalaspis* by the general configuration of its cephalic shield, the shortness of the cornua and the absence of real denticles on them, the narrowness of the pectoral sinuses and by the great breadth of the inter-zonal part.

Geological Formation and Locality.—Lower Old Red Sandstone (? Downtonian): Oban and I. of Kerrera, Argyllshire.

10. *Cephalaspis lyelli* Agassiz.

(Text-fig. 40; Pl. 15, fig. 1.)

1835. *Cephalaspis lyellii*, L. Agassiz, p. 142, pl. i*a*, fig. 2 (no other figures).
1839. *Cephalaspis lyellii*, R. I. Murchison, p. 589, pl. i, fig. 2 (*non* pl. i, fig. 1; pl. ii, figs. 1, 2).
1870. *Eucephalaspis lyellii*, E. R. Lankester, pp. 43–46, pl. viii, fig. 1 (? pl. xi, figs. 1, 2).
1891. *Cephalaspis lyelli*, A. S. Woodward, pp. 179–181 (specimens nos. 20087 and P. 3233 only).
1903*a*. *Cephalaspis lyellii*, W. Patten, p. 847, etc., pl. ii, fig. 6 (*non* pl. i, fig. 2).

Diagnosis.—A *Cephalaspis* with total length of adult probably between 20 and 30 cm. Cephalic shield measuring between one-third and one-fourth of total length. Maximum breadth of cephalic shield, measured across posterior parts of cornua, about equal to length of cephalic shield in median line. Cornua projecting backwards and slightly laterally, well developed, their length contained about three and one-third times in distance of their tips from rostral margin of cephalic shield; inner margins of cornua probably without denticles but with pectoral angles. Pectoral sinuses rather narrow. Inter-zonal part rather short and narrow and without dorsal spine. Orbital openings not especially large, situated near middle of length of cephalic shield in median line, but much nearer to pectoral sinuses than to rostral margin. Dorsal electric field about three times as long as broad. Dorsal crest of trunk consisting of about 8–10 scutes. Posterior dorsal fin beginning above 28–30th transverse rows of scales. Exoskeleton with (?) continuous superficial layer. Mucous canals probably enclosed in exoskeleton.

Lectotype.—Imperfect cephalic shield and associated trunk, partly in counterpart, in the British Museum (nos. 20087 and P. 3233); specimen chosen by E. R. Lankester (1870, pp. 43–45) by elimination.

Material.—The available material which may be definitely referred to this species consists only of the lectotype and its counterpart. Otherwise there are only two cephalic shields (nos. P. 6945 and P. 6945*a*, in the British Museum) which resemble the lectotype sufficiently to be placed in *C. lyelli* even with hesitation.

As is well known from earlier descriptions (Agassiz 1835; Lankester 1870; and Woodward 1891), the lectotype displays not only the cephalic shield but also the scale-covered division of the trunk, except the caudal part. The specimens doubtfully referred to this species are represented only by detached and rather fragmentary cephalic shields.

Description.—This is the genotype of *Cephalaspis*. The lectotype is about 25 cm. in total length and it was thus of medium size.

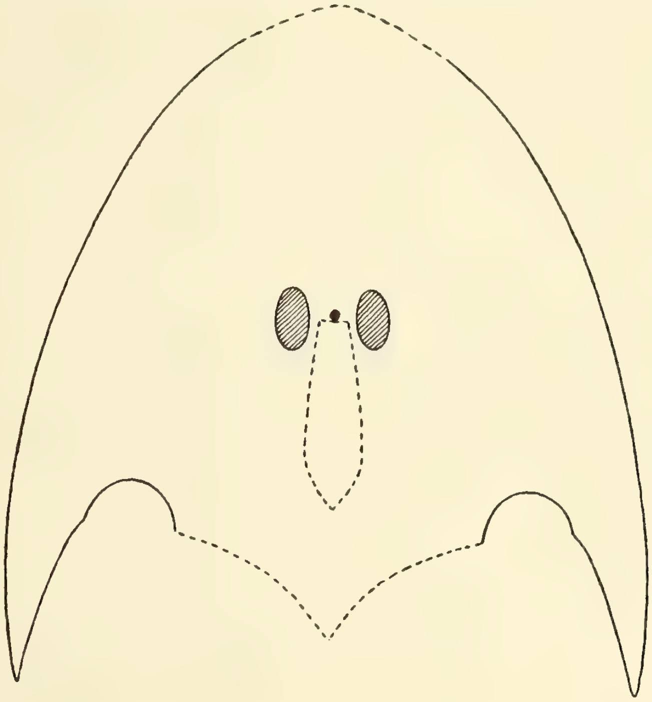
The cephalic shield of the lectotype is about 7·8 cm. long from the rostral end to the posterior margin of the inter-zonal part, and its length thus constitutes between one-third and one-fourth of the total length of the specimen. Its maximum breadth, which is situated across the posterior parts of the cornua, was about 8 cm., and it thus exceeded its length but slightly. Its maximum height, which, as usual, lies far back in the inter-zonal part, can only be estimated at 1·8 cm. or perhaps a little more. The distance from the posterior end of each cornu to the rostral end of the shield is about 9·5 cm. The inter-zonal part at the posterior end measures about 3·6 cm. in breadth, which thus constitutes somewhat less than one-half the maximum breadth of the shield.

Taken as a whole, the cephalic shield of the lectotype is fairly narrow in proportion to its length. The most rostral part is not complete and thus it is impossible to be certain whether a rostral angle was present, though it seems likely that it was. The cornua, which are directed slightly laterally, are fairly robust and seem to have been rather flat dorso-ventrally. They are about 3 cm. long, and their length is thus only slightly less than one-third of the distance between their tips and the rostral end of the cephalic shield. Their inner margins are, at least in the present state of preservation, without distinct denticles, but seem to have had small and not very distinct pectoral angles. The pectoral sinuses are well defined but rather narrow. The inter-zonal part is fairly short and has on its dorsal side a low median crest, but no dorsal spine, as is plainly shown by the counterpart of the lectotype. The orbital openings, which are fairly small and oval in shape, are situated near the middle of the length of the cephalic shield, but they are, of course, much nearer to the anterior end of either pectoral sinus than to the rostral margin, or, more correctly, to the supposed rostral angle. The dorsal electric field is not well preserved, but although its exact shape cannot be made out, one may clearly see that it was rather long, and that its maximum breadth, which is about one-third its length, is situated far backwards and that from this point forwards the field decreases very gradually in breadth. The lateral electric fields are so imperfectly preserved that nothing is known of their shape and extent.

The endoskeleton of the cephalic shield of the lectotype is imperfect, but it is clear, however, that at least some of the perichondrial bone-layers were present, such as the orbital and labyrinth layers and those which lined the nerve-canals of the lateral electric fields.

The exoskeleton of the cephalic shield of the lectotype is much weathered and therefore not in a condition suited for detailed study. It seems most likely, however, that the superficial layer formed a continuous covering to the middle layer. The nature of the ornamentation is so far unknown.

Of the mucous canal system nothing is to be seen in the lectotype, but it seems likely that it was entirely enclosed in the exoskeleton.



Text-fig. 40.—*Cephalaspis lyelli* Agassiz. Cephalic shield in dorsal view. After the lectotype, specimen no. 20087 in the British Museum. Nat. size.

The cephalic shields doubtfully referred to this species are both imperfectly preserved (Pl. 15, fig. 1). In most respects they seem to agree with the cephalic shield of the lectotype, but the more complete specimen apparently differs from that by a somewhat shorter inter-zonal part and by the absence of a pectoral angle on the cornua. The other shield lacks both cornua, but its inter-zonal part seems to be proportionately as long as that of the lectotype.

The trunk of the lectotype is so exposed that all is accessible for investigation except the under-surface, by which it is attached to the matrix. Its shape, which seems to have been rather well preserved, is distinctly triangular in cross-section, and decreases rather rapidly both in height and breadth towards the tail.

The pectoral fins of the lectotype are in a bad state of preservation, but it is clear that they were well developed and rather broad. As in *Hemicyclaspis murchisoni*, *Cephalaspis pagei* and *C. powriei*, they are covered by numerous small scales. The detailed structure and arrangement of these scales cannot, however, be seen.

The anterior dorsal fin of the lectotype is, as in *H. murchisoni*, represented by a high dorsal crest consisting of an unpaired series of dorsal scutes. These scutes seem to be about eight or ten in number, and the most posterior of them is, just as in *H. murchisoni*, much longer than the others : its posterior end reaches as far backwards approximately as the level of the 21st transverse row of scales.

The posterior dorsal fin of the lectotype, which commences at the level of the 28th or 30th transverse row of scales, has its usual remote position. Its anterior border is, as in *C. pagei* and *C. powriei*, strengthened by a spine, consisting of a number of independent pieces rigidly fixed together.

The caudal fin of the lectotype is unknown at the moment, but it is not impossible that it is preserved although it has not been exposed.

The squamation of the lectotype is essentially as in *Hemicyclaspis murchisoni*, *C. pagei* and *C. powriei*, but the transverse rows of scales are broader and the high lateral scales somewhat lower than in those species, the most anterior of the high lateral scales being in *C. lyelli* only about five times as high as broad. The ventrolateral scales are well developed and at the transition to the caudal region are still of the same height as in the abdominal region. The nature of the ornamentation of the scales cannot be determined, for their superficial and middle layers are not preserved.

REMARKS.—The species *C. lyelli* was based by AGASSIZ in 1835 on several specimens, both from England and Scotland. LANKESTER in 1870 undertook a revision of the species, by which it was so limited as to comprise only the specimen figured by AGASSIZ in Pl. 1*a*, fig. 2, which was from Glammis, Forfarshire, and a second specimen from near Arbroath in the same county. LANKESTER thus chose the Glammis specimen figured by AGASSIZ as lectotype of the species.

In 1891, in his Catalogue, WOODWARD (1891, pp. 179–181) united the species *C. agassizi*, established by LANKESTER in 1870 (pp. 46–47, Pl. 9, figs. 2, 3, 6), with *C. lyelli*, and in addition he also assigned to this species a number of other specimens both from English and Scottish localities.

The knowledge which we now possess of the Cephalaspids in general makes it, however, obvious that *C. lyelli* must comprise only the lectotype and perhaps a few other Scottish specimens. Whether the Arbroath specimen, which, as mentioned above, was ascribed by LANKESTER to *C. lyelli*, really has anything to do with this I am unable to say, as I have not had the opportunity of studying it.

As far as it is known at present *C. lyelli* is especially characterized by its relatively narrow cephalic shield, by the fairly short cornua, which, at least in several specimens, have pectoral angles, by the fairly narrow pectoral sinuses, the rather short interzonal part without a dorsal spine, the position of the orbit rather far back relatively to the pectoral sinuses, the long and somewhat narrow dorsal electric field decreasing in breadth but slightly towards the front, the breadth of the transverse rows of scales and by the relative shortness of the high lateral scales.

The specimens from the Gedinnian of the Pas-de-Calais figured by Leriche (1906, p. 37, Pl. iv, figs. 6, 7) are not of this species.

Geological Formation and Localities.—Lower Old Red Sandstone: Glammis (lectotype) and Brechin (doubtful specimens), Forfarshire.

11. *Cephalaspis lankesteri*, sp. nov.

(Text-fig. 41; Pl. 17, figs. 2, 3; Pl. 56, fig. 2.)

1870. *Eucephalaspis agassizi* (in part), E. R. Lankester, pp. 46–47, pl. viii, fig. 2.
1891. *Cephalaspis lyelli* (in part), A. S. Woodward, p. 179.

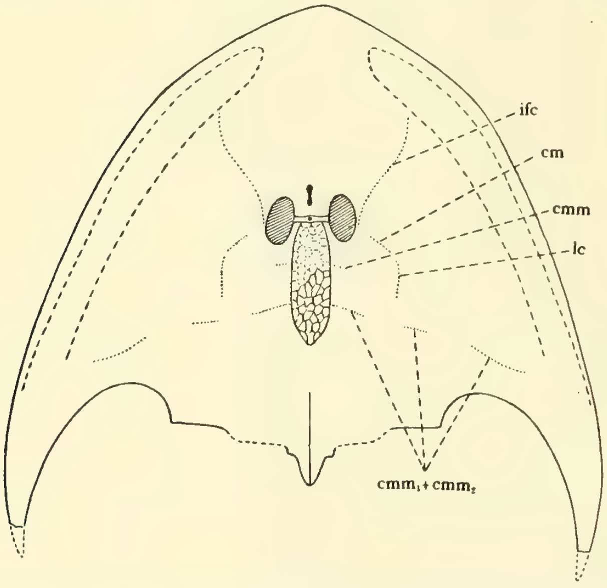
Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across middle parts of cornua, somewhat greater than length of cephalic shield in median line. Rostral angle well developed. Rostral margin separated from lateral margins by obtuse angles. Cornua projecting backwards and slightly laterally, moderately stout and of medium length, constituting about one-third only of distance of their tips from rostral angle; outer margins of cornua strikingly convex; inner margins without denticles and pectoral angles. Pectoral sinuses rather broad and somewhat shallow. Inter-zonal part short, fairly narrow and with low, backwardly inclined dorsal spine. Orbital openings of moderate size, situated slightly in front of middle of the length of cephalic shield and nearly midway between rostral angle and pectoral sinuses. Dorsal electric field about three times as long as broad. Lateral electric fields reaching backwards on to cornua. Exoskeleton with continuous superficial layer and probably without tubercular ornamentation. Mucous canal system enclosed in exoskeleton and forming uniformly fine-meshed network.

Holotype.—Cephalic shield partly in counterpart, in the British Museum (nos. 45943 and P. 16155), Pl. 17, figs. 2, 3; Pl. 56, fig. 2.

Material.—The only available material of this species is the holotype, which was figured by Lankester in 1870 in Pl. 9, fig. 2, and its fragmentary counterpart.

Description.—The length of the holotype from the rostral margin to the posterior end of inter-zonal part is about 6·3 cm. The maximum breadth, which is approximately across the middle of the cornua, cannot be directly measured, as the shield is imperfect on the left side, but it may be estimated at about 7 cm. or rather more; and thus, as in *C. lyelli*, it exceeded the length but slightly. The maximum height, which, as usual, is far back in the inter-zonal part, is about 3 cm. with, and about 3·5 cm. without, the dorsal spine, and is thus unusually great in proportion both to the length and maximum breadth; but as the shield is slightly laterally compressed, the maximum breadth was originally a little greater, and the maximum height a little less, than in its present state. The distance from the tip of each cornu to the rostral end of the shield is about 8·2 cm. Finally, the inter-zonal part is in its present state of preservation 3·1 cm. broad posteriorly, but as the shield is somewhat compressed laterally it was originally probably a little broader.

The rostral margin of the shield, which forms a very distinct rostral angle, is bounded on each side by an obtuse but moderately conspicuous angle. The cornua project somewhat laterally and are fairly robust and rather flat dorso-ventrally. In addition, they are somewhat curved inwards and have neither denticles nor pectoral angles. The length of the cornua, which is about 2·7 cm., constitutes about a third of the distance from their tips to the rostral angle. The pectoral sinuses are well defined and somewhat broader than in *C. lyelli*. The inter-zonal part is short, as in *C. lyelli*, but, contrary to what is the case in that species, it bears a dorsal spine, which, though it is not especially high, is nevertheless very distinct. In breadth the inter-zonal part seems to have been very much as in *C. lyelli*. The orbital openings, which are oval in shape and fairly small, lie further forwards than in the other species, both in relation to the rostral angle and the posterior end of the inter-zonal part and to the pectoral sinuses. The dorsal electric field is long and narrow, its maximum breadth constituting only about a third of the length, resembling in this and in its general shape that in *C. lyelli*. The small exoskeletal plates covering the field are partly well preserved (Pl. 17, fig. 2). The lateral electric fields have their usual shape, and reach somewhat backwards on to the cornua.



Text-fig. 41.—*Cephalaspis lankesteri*, sp. nov. Cephalic shield in dorsal view. After the holotype and counterpart, specimens nos. 45943 and P. 16155 in the British Museum. Nat. size.
For explanation of lettering see text-fig. 23.

Little can be seen of the endoskeleton of the shield. As far as can be judged, however, it is likely that it was very imperfectly ossified.

The exoskeleton of the shield is well preserved and it is clear that its superficial layer was continuous and, at least on the dorsal side of the shield, quite smooth, without traces of tuberculation.

The mucous canal system of the shield is entirely enclosed in the exoskeleton. The inter-areal canals form a fine plexus which agrees so closely with that of the intra-areal canals as to be indistinguishable from it (Pl. 56, fig. 2), the whole system being uniformly fine-meshed.

The sensory grooves are partly well preserved in the counterpart (Pl. 17, fig. 3), and as far as they can be seen are shown in text-fig. 41.

Remarks.—The shield described here was referred by Lankester to *C. agassizi*. It is evident, however, from what we now know that it cannot be retained in that species (see pp. 125–127), but that it represents a new species which I have named in honour of the late Sir E. Ray Lankester.

C. lankesteri is distinguished especially by the following characters of the cephalic shield : the presence of a pronounced rostral angle and an angle between the rostral and each lateral margin ; the shape and curvature of the cornua ; the absence of denticles on the inner margins of the cornua ; the breadth of the pectoral sinuses ; the shortness of the inter-zonal part ; the presence of a well-developed, backwardly inclined dorsal spine ; the anterior position of the orbital openings ; the long and narrow shape of the dorsal electric field ; the presence of a continuous superficial layer of the exoskeleton; the absence of tubercular ornamentation; and the development of the mucous canal system.

C. lankesteri, as here defined, is undoubtedly closely related to *C. lyelli*, *C. fletti* and *C. cradleyensis*, but differs from each of these in several characters.

Geological Formation and Locality.—Lower Old Red Sandstone: Whitbach, Shropshire.

12. *Cephalaspis agassizi* Lankester.

(Text-fig. 42; Pl. 16, figs. 3, 4; Pl. 22, figs. 3, 4.)

1870. *Eucephalaspis agassizi* (in part), E. R. Lankester, p. 46, pl. ix, fig. 6 (*non* figs. 2, 3; *nec* pl. viii, fig. 5).
1891. *Cephalaspis lyelli* (in part), A. S. Woodward, pp. 179–180 (specimen no. 42140).
1891. *Cephalaspis salweyi* (in part), A. S. Woodward, p. 182 (specimen no. 33319).

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across posterior parts of cornua, somewhat less than length of cephalic shield in median line. Rostral parts of cephalic shield fairly narrow. Rostral angle rather indistinct. Cornua projecting somewhat laterally, and fairly slender, their length contained almost three times in the distance of their tips from rostral angle; inner margins of cornua with small, straight or forwardly curved denticles. Pectoral sinuses broad and deep. Inter-zonal part narrow, strikingly long and with low, fairly indistinct, dorsal spine. Orbital openings not especially large, situated in front of middle of length of cephalic shield. Dorsal electric field about three times as long as broad. Lateral electric fields reaching a little way backwards on to cornua, and pointed posteriorly. Exoskeleton with superficial layer discontinuous. Ornamentation consisting of tubercles, often of two sizes, either fairly coarse or rather small. Mucous canal system situated entirely superficially to exoskeleton.

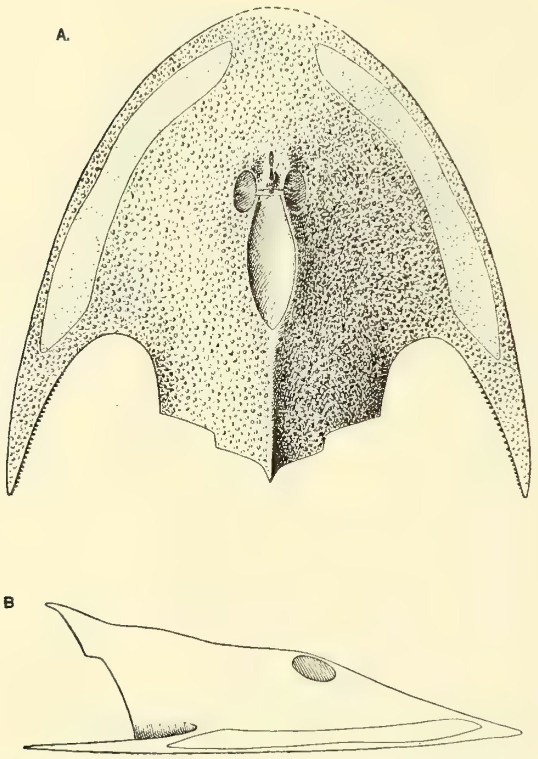
Lectotype.—Cephalic shield, in the University Museum, Oxford (specimen figured by Lankester, 1870, Pl. 9, fig. 6), Pl. 16, fig. 3; hereby chosen.

Material.—The material which I place in this species consists of seven specimens. Of these three belong to the British Museum (nos. 33319, 42140 and P. 14550); two to the Museum of Practical Geology, London (nos. 47815, 47816); one to the Royal Scottish Museum, Edinburgh (no. 1891.99.12); and one to the University Museum, Oxford (not numbered).

All the available specimens consist of more or less fragmentary cephalic shields only.

As lectotype I choose the specimen belonging to the University Museum of Oxford. This is one of the specimens on which Lankester (1870, pp. 46, 47; Pl. 9, fig. 6) founded this species.

Description.—The lectotype is distorted by pressure in the rock so that it is somewhat longer and narrower than in its original condition. Its dimensions are as follows: length from the rostral margin to the posterior margin of the inter-zonal part, 6 cm.; maximum breadth (across the posterior parts of the cornua), 6 cm. (originally about 7 cm.); maximum height, 1·5 cm.; breadth of inter-zonal part posteriorly, 2·5 cm. (originally about 3 cm.); length of the cornua, 2·4 cm.; and distance from the tips of the cornua to the rostral end of the shield, 7 cm. The best-preserved shield, which belongs to the Museum of Practical Geology, London (no. 47815), has the following dimensions: length from the rostral margin to the posterior margin of the inter-zonal part, 5·7 cm.; maximum breadth (across the posterior parts of the cornua), 7 cm.; maximum height, 1·5 cm.; breadth of inter-zonal part posteriorly, 3 cm.; length of cornua (incomplete), 2·3 cm.; distance from tips of the cornua to the rostral end of the shield, 7·4 cm. The other four shields are of approximately the same size as the foregoing, so that the species seems to have attained but a moderate size.



Text-fig. 42.—*Cephalaspis agassizi* Lankester. Cephalic shield. A, dorsal view; B, lateral view. Mainly after the lectotype, in the University Museum, Oxford. Nat. size.

The rostral part of the shield is fairly narrow. Its rostral margin, which is preserved only in one of the two specimens belonging to the Museum of Practical Geology, exhibits but slight evidence of a rostral angle. The cornua, which project posteriorly and slightly laterally, are slender and rather long, their length being contained somewhat less than three times in the distance from their tips to the rostral angle. Their inner margins are provided with relatively small denticles, which are straight or slightly curved forwards. The pectoral sinuses are deep but fairly broad. The inter-zonal part is strikingly long and provided dorsally with a distinct median crest, which is produced posteriorly into a very low, but not very conspicuous, dorsal spine. The orbital openings are small and situated somewhat nearer the rostral end of the shield than the posterior end of the inter-zonal part. The dorsal electric field is long and narrow, its breadth constituting only about a third of the length. The lateral electric fields reach a little way backwards on to the cornua.

Of the endoskeleton only very fragmentary remains are to be found, consisting of the following perichondrial bone-layers: the orbital, the internal, the external, and certain canal-layers.

The exoskeleton of the cephalic shield is well developed but its superficial layer is not continuous. The ornamentation of the dorsal side of the shield consists of pointed tubercles, which, at least in some specimens, are of two fairly distinct sizes, being either small or fairly large. In some specimens these tubercles are somewhat rounded, in others slightly elongated, and most posteriorly on the inter-zonal part slightly inclined backwards. Apparently the tubercles are rather irregularly arranged on the entire dorsal side of the shield. The ornamentation of the ventral rim is very imperfectly known, but as far as it could be studied it seems to be similar to that on the dorsal side of the shield.

The mucous canal system of the cephalic shield lay superficially to the exoskeleton, so that there are no distinct grooves or markings.

REMARKS.—When LANKESTER in 1870 established this species he referred to it all the English specimens suggestive of *C. lyelli*, in which, as already pointed out, he placed certain Scottish specimens only. WOODWARD in 1891 considered it impossible to retain *C. agassizi* as a distinct species and united it with *C. lyelli*.

From the facts now known it is clear not only that the specimens referred by LANKESTER in 1870 to *C. agassizi* are specifically distinct from *C. lyelli*, but also that they belong to two different species. According to current rules of nomenclature, the specific name *C. agassizi* has thus to be applied to one of these two species. LANKESTER unfortunately did not indicate which of the specimens figured by him under the name *C. agassizi* was to be considered as a holotype, but since it is obvious that the restoration which he gives of the cephalic shield of this species (1870, text-fig. 11) is undoubtedly to a large extent based on the specimen which he figured in pl. 9, fig. 6, I have chosen this as the lectotype of *C. agassizi*. The specimen figured at the same time by LANKESTER in pl. 9, fig. 2 is the holotype of a new species which I name *C. lankesteri* (see p. 123).

C. agassizi with its present definition is a very well characterized species, which cannot be confused with any other. It is distinguished especially by the deep and well-developed pectoral sinuses, the strikingly long and rather narrow inter-zonal part, the very low and indistinct dorsal spine, the forward position and small size of the orbital openings, the long and narrow dorsal electric field, the ornamentation, and finally the position of the mucous canal system superficially to the exoskeleton.

As far as can be judged, *C. agassizi* does not seem to be very closely related to any of the known British or Spitsbergen Cephalaspids.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: Whitbach and near Ludlow (see p. 198), Shropshire; Cradley, Herefordshire; Skirrid Fawr, Monmouthshire.

13. *Cephalaspis fletti*, sp. nov.

(Text-fig. 43; Pl. 15, figs. 2–4; Pl. 16, fig. 2; Pl. 18, fig. 2; Pl. 22, figs. 1, 2; Pl. 59, fig. 2.)

1891. *Cephalaspis lyelli* (in part), A. S. Woodward, pp. 179–181 (? specimen no. P. 3235).

DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across anterior halves of cornua, somewhat less than length of cephalic shield in median line. Rostral part of cephalic shield rather narrow. Rostral angle well developed. Cornua projecting directly backwards, of moderate length, this being contained only about three times in distance of their tips from rostral angle; inner margins of cornua with pointed, forwardly curved denticles. Pectoral sinuses narrow. Inter-zonal part short, rather broad and probably with low, backwardly inclined dorsal spine. Orbital openings of moderate size or rather small, situated in front of middle of length of cephalic shield and almost midway between rostral angle and pectoral sinuses. Dorsal electric field about two and a half times as long as broad. Lateral electric fields extending somewhat backwards on to cornua and pointed posteriorly. Exoskeleton with continuous superficial layer. Dorsal side of cephalic shield smooth. Rostral margin, lateral margins and ventral rim with numerous small tubercles, except on outer margins of cornua, where they are somewhat larger. Mucous canal system enclosed in exoskeleton and probably forming fine-meshed network.

HOLOTYPE.—Cephalic shield, in the Ludlow Museum (no. 1), Pl. 15, fig. 3; Pl. 22, fig. 2.

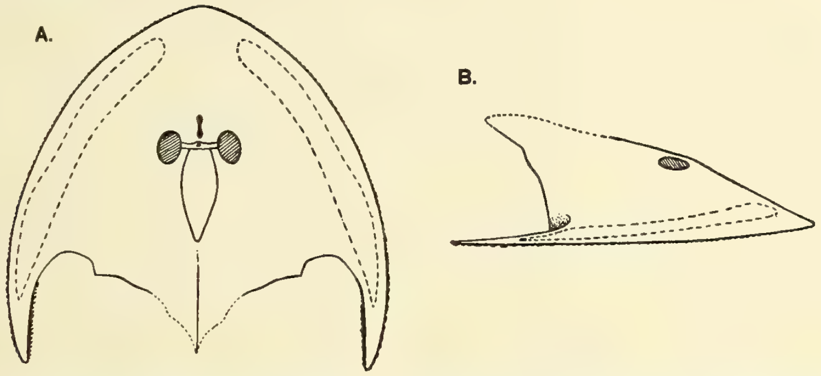
MATERIAL.—The material which can be placed in this species with a reasonable degree of certainty consists of three specimens, belonging to the Museum of Practical Geology, London (no. 47809), the Ludlow Museum (the holotype) and Mr. Wickham King (now in the British Museum, no. P. 16139). In addition to these specimens I also refer to the species under consideration, though with hesitation, four specimens, one of which belongs to the British Museum (no. P. 3235), two to the Museum of Practical Geology (nos. 6474, 47811) and one to the Ludlow Museum (no. 6). All these specimens are detached cephalic shields in a more or less imperfect state of preservation.

DESCRIPTION.—The length of the cephalic shield from the rostral end to the posterior margin of the inter-zonal part is from 4 to 4·7 cm. The maximum breadth, which is approximately across the anterior halves of the cornua, varies from about 4·9 cm. in the smallest shields to about 5·3 cm. in the largest. The maximum height, which in the normal way is situated at the hinder end of the inter-zonal part, is from 1·5 cm. to about 1·9 cm., excluding the dorsal spine, the height of which seems to be about 0·3 or 0·4 cm. The distance from the tip of each cornu to the rostral end of the shield measures between 5·2 and 6 cm. Finally, the breadth of the inter-zonal part at the hinder end varies from about 2·6 to 3·1 cm. All the available shields are thus from fairly small individuals.

The rostral part of the shield is rather pointed and a distinct rostral angle is developed. The cornua, which project almost straight backwards, are well developed, and their length is contained about three times in the distance from their tips to the rostral angle of the shield. In the holotype and in some other specimens they are curved somewhat inwards; in the remainder they are straight. Their inner margins are provided with a series of fairly well developed, conical denticles, all of which are curved somewhat forwards. The lateral margins of the cornua bear fairly large, but very obtuse tubercles, which form the posterior continuation of the series along the rostral and lateral margins of the shield. Pectoral angles do not seem to be present. The pectoral sinuses, which are well defined, are narrow. The inter-zonal part is short and broad, although in the holotype this is so imperfectly preserved dorsally that its form cannot be seen. In some of the doubtful specimens it is clearly provided with a low, backwardly inclined dorsal spine. The orbital openings, which are not particularly large, are situated somewhat in front of the middle of the shield, and, as in *C. agassizi*, they lie considerably further from the pectoral sinuses than in *C. lyelli*. The dorsal electric field is relatively broader than in *C. lyelli* and *C. lankesteri*, its breadth being contained two and a half times or slightly less in its length: otherwise this field is characterized by the position of its maximum breadth at about the middle of its length and the slight diminution in breadth forwards. The lateral electric fields are well developed and seem to reach backwards on to the cornua.

Of the endoskeleton of the cephalic shield most specimens display but little. In one specimen, however, there are remains of the part of the external perichondrial bone-layer lining the oralo-branchial chamber.

The exoskeleton of the cephalic shield is well developed and has a continuous superficial layer. On the dorsal side of the shield it seems to have been entirely, or almost entirely, smooth; but on the ventral rim and along the rostral and lateral margins it is ornamented with numerous, very obtuse tubercles, which are small, except posteriorly on the outer margins of the cornua, where, as already pointed out, they are fairly large.



Text-fig. 43.—*Cephalaspis fletti*, sp. nov. Cephalic shield. A, dorsal view; B, lateral view. After the holotype, specimen no. 1 in the Ludlow Museum. Nat. size.

The mucous canal system is entirely enclosed in the exoskeleton. On the cornua, the only places where it could be studied in detail, it consists throughout of a fine-meshed plexus of canals, its inter-areal canals being there developed similarly to the intra-areal canals.

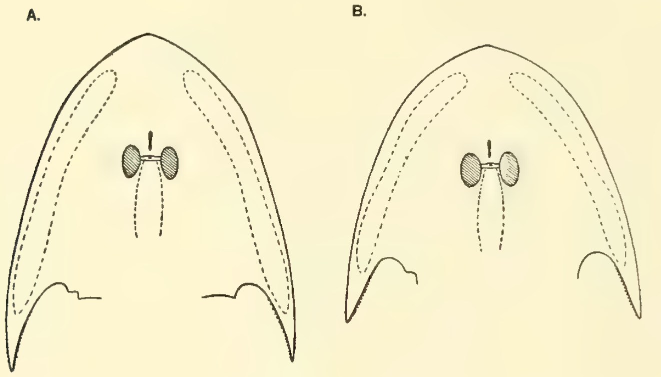
Remarks.—This species is on the whole rather suggestive of *C. lyelli*, *C. lankesteri*, *C. cradleyensis*, *C. whitbachensis* and *C. websteri*. It differs, however, from all these by its moderate size, the general shape of the cephalic shield, the absence of pectoral angles on the cornua, the presence of forwardly inclined, conical denticles on the inner margins, and of fairly large obtuse tubercles along the outer margins of the cornua, the narrowness of the pectoral sinuses, the relatively great breadth of the inter-zonal part, the presence of a low but distinct dorsal spine on the inter-zonal part and the development of the ornamentation. It has been named in honour of Sir John Flett, the Director of the Geological Survey of Great Britain.

Geological Formation and Localities.—Lower Old Red Sandstone: Downton Hall, Shropshire; Leverhill and (?) Cradley, Herefordshire; Guildings Brook, Trimpley, Worcestershire.

14. *Cephalaspis cradleyensis*, sp. nov.

(Text-fig. 44; Pl. 15, fig. 6.)

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across posterior parts of cornua, probably not much greater than length of cephalic shield in median line. Rostral angle well developed. Cornua projecting somewhat laterally, short, their length constituting only about one-fourth of distance of their tips from rostral angle; inner margins of cornua with small, pointed, forwardly inclined denticles. Pectoral sinuses narrow. Inter-zonal part broad and probably short. Orbital openings rather large and situated at, or slightly in front of, middle of length of cephalic shield. Dorsal electric field about three times as long as broad. Lateral electric fields reaching backwards on to cornua. Ornamentation of numerous, small, flat tubercles on rostral and lateral margins and ventral rim of cephalic shield.



Text-fig. 44.—*Cephalaspis cradleyensis*, sp. nov. Attempted restorations of the cephalic shield in dorsal view, based on the assumption that the length was that of A, the longest side of the holotype, B, the shortest side of the holotype. After the holotype, specimen no. P. 5375 in the British Museum. Nat. size.

Holotype.—Cephalic shield, in the British Museum (no. P. 5375), Pl. 15, fig. 6.

Material.—This species is founded on the holotype alone, an imperfectly preserved cephalic shield.

Description.—This cephalic shield is distorted so that its left side is shorter than its right, but otherwise it seems to have retained its original shape. Its dimensions are as follows: the length from the rostral margin to the posterior end of the inter-zonal part cannot be directly measured, but it may be estimated at 3·5 cm. or perhaps a little more; the maximum breadth, which lies between the posterior ends of the cornua, is about 3·9 cm., and thus does not greatly exceed the length. The maximum height seems to be about 1·2 cm. excluding the dorsal spine. The distance from the tips of the cornua to the rostral end of the shield is 4·6 cm. on the right side and 4 cm. on the left. Finally, the inter-zonal part is 2 cm. broad. This cephalic shield is therefore from a small individual.

Taken as a whole, the cephalic shield is narrow, but from its state of preservation it seems probable that originally it was somewhat wider than it is now. A distinct rostral angle is present. The cornua project somewhat laterally and are strikingly short, their length being equal to only one-fourth of the distance between their tips and the rostral angle. They are, moreover, fairly straight and bear conical, forwardly inclined denticles along their inner margins. The pectoral sinuses are well defined but narrow. The inter-zonal part is fairly broad, constituting about one-half of the maximum breadth of the cephalic shield. The dorsal side of the inter-zonal part is imperfectly preserved, so that it is impossible to determine whether a dorsal spine was developed or not. The orbital openings, which are fairly large and oval in shape, are situated somewhat in front of the middle of the length of the shield in the median line. Their distance in front of the pectoral sinuses is, as in *C. fletti*, distinctly greater than in *C. lyelli*. The dorsal electric field seems to have been about three times as long as broad. The lateral electric fields reach rather far backwards on to the cornua.

Of the endoskeleton scarcely anything is to be seen. The exoskeleton is so imperfectly preserved that it is impossible to ascertain whether the superficial layer was continuous or not. The ventral rim and the rostral and lateral margins of the shield are ornamented with numerous small flat tubercles, but the ornament of the dorsal side of the shield is entirely unknown.

Owing to the imperfect state of preservation of the exoskeleton, nothing is known of the position and development of the mucous canal system.

REMARKS.—The cephalic shield described here resembles in several respects that of *C. fletti*. It differs, however, from that especially by its generally different shape, its much shorter and more laterally directed cornua, and by its much longer and narrower dorsal electric field. As far as can be seen at present, therefore, this shield must be considered to represent a distinct species, which I have named *C. cradleyensis*, after the locality at which it was found.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Cradley, Herefordshire.

15. *Cephalaspis whitbachensis*, sp. nov.

(Text-fig. 45; Pl. 15, fig. 5.)

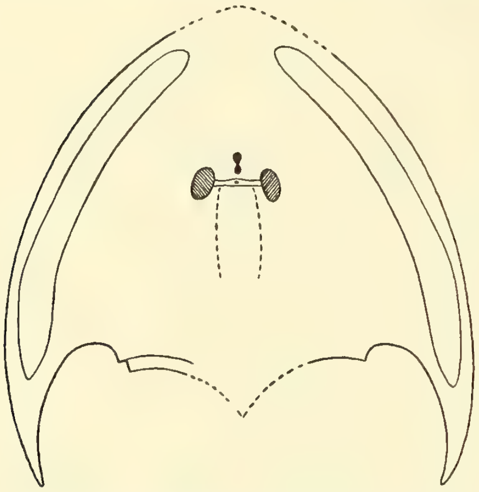
DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across anterior parts of cornua, somewhat greater than length of cephalic shield in median line. Cornua projecting directly backwards and rather strongly curved inwards, fairly short, their length being contained about three and a half times in distance of their tips from rostral end of cephalic shield; inner margins of cornua without denticles. Pectoral sinuses narrow. Inter-zonal part short and broad. Orbital openings small and situated slightly in front of middle of length of cephalic shield. Dorsal electric field probably about three times as long as broad. Lateral electric fields reaching backwards on to cornua. Exoskeleton with continuous superficial layer and probably smooth. Mucous canal system enclosed in exoskeleton.

HOLOTYPE.—Cephalic shield, in Ludlow Museum (no. 7), Pl. 15, fig. 5.

MATERIAL.—This species is based on a single specimen, which consists of an imperfect cephalic shield only.

DESCRIPTION.—The dimensions of the holotype are as follows: the length between the rostral and posterior ends cannot be measured exactly, but it is obvious that it cannot have been much less or much greater than 5 cm.; the maximum breadth, which is between the anterior parts of the cornua, measures 6·2 cm.; the maximum height, excluding the dorsal spine, if any, seems to have been nearly 2 cm.; the distance from the posterior end of each cornu to the rostral end of the shield is about 6·8 cm.; finally, the breadth of the inter-zonal part at its hinder end measures 3·2 cm.

The rostral margin of the shield is so imperfectly preserved that one cannot be sure whether a rostral angle was present or not. The cornua, which project almost directly backwards and are markedly curved inwards, are fairly short, their length being contained about three and a half times in the distance from their tips to the rostral end of the shield; their inner margins bear no denticles. The pectoral sinuses are well defined but narrow. The inter-zonal part is short and fairly broad, but whether it bore a dorsal spine it is impossible to say, as its dorsal portion is lacking. The orbital openings are strikingly small in proportion to the size of the shield and are situated slightly in front of the middle of its length. Although the dorsal electric field is not completely preserved, it is clear that it was long and narrow, its breadth being only about one-third of its length, and its maximum breadth situated about the middle of its length, from which point it diminishes but slightly forwards. The lateral electric fields reach rather far backwards on to the cornua. Some of the exoskeletal plates covering the field of the left side are preserved.



Text-fig. 45.—*Cephalaspis whitbachensis*, sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. 7 in the Ludlow Museum. Nat. size.

Of the endoskeleton only some of the perichondrial bone-layers lining the canals of the nerves of the lateral electric fields and certain canals of the sub-aponeurotic (sub-cutaneous) vascular plexus are to be seen.

The exoskeleton is provided with a continuous superficial layer, which, at least on the ventral rim and on the rostral and lateral margins, seems to be smooth, or without distinct tubercles.

The mucous canal system is completely enclosed in the exoskeleton. Its development otherwise is unknown.

Remarks.—The cephalic shield described here is especially suggestive of that of *C. fletti*. From that it differs, however, by the absence of denticles on the inner margins of the cornua, by smaller and more forwardly situated orbital openings, and by the absence of tubercles on the ventral rim and rostral and lateral margins. It also resembles the shield of *C. lankesteri*, but its general shape is different, the cornua shorter, and the pectoral sinuses narrower. It is also suggestive of that in *C. cradleyensis*; from this it is distinguished, however, by its longer cornua, the absence of denticles on the inner margins of the cornua, smaller and somewhat differently situated orbital openings, and by the absence of tubercles on the ventral rim and along the rostral and lateral margins. It does not greatly resemble the shield of any other known form, and thus I have described it as the type of a new species, which I have called *C. whitbachensis*, from the locality at which the holotype was found.

Geological Formation and Locality.—Lower Old Red Sandstone: Whitbach, Shropshire.

16. *Cephalaspis websteri*, sp. nov.

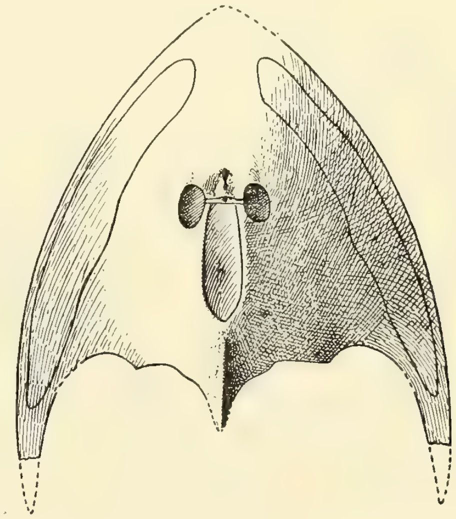
(Text-fig. 46; Pl. 17, fig. 1.)

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across anterior parts of cornua, about equal to length of cephalic shield in median line. Rostral part of cephalic shield narrow, probably with rostral angle. Cornua slender, projecting directly backwards; their length contained from three to four times in distance of their tips from rostral end of cephalic shield; inner margins of cornua probably without denticles. Pectoral sinuses shallow and broad. Inter-zonal part short and narrow, with rather high, almost vertical dorsal spine. Orbital openings situated about middle of length of cephalic shield, but much nearer to pectoral sinuses than to rostral end of cephalic shield. Dorsal electric field about three times as long as broad. Lateral electric fields reaching backwards on to cornua.

Holotype.—Impression of dorsal surface of a cephalic shield, in the British Museum (no. P. 16150), Pl. 17, fig. 1.

Material.—This species is based on a single specimen, consisting of a cephalic shield preserved as an imperfect impression of the dorsal surface.

Description.—The cephalic shield measures about 7 cm. in length from the rostral end to the posterior end of the inter-zonal part, and has a maximum breadth, between the anterior parts of the cornua, of 7·5 cm., or perhaps slightly more. As the shield is somewhat compressed dorso-ventrally, the maximum height, which measures about 1·5 cm. without the dorsal spine, is certainly somewhat smaller in the fossil than it was originally. For the same reason the maximum breadth is conceivably larger than it was in life. The distance from the tip of each cornu to the rostral margin cannot be definitely ascertained on account of the imperfect state of preservation, but as far as can be judged it was at least 9 cm. The breadth of the inter-zonal part likewise cannot be directly measured, but it may be estimated at 3·5 cm. at the hinder end. The specimen was thus of medium size.



Text-fig. 46.—*Cephalaspis websteri*, sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. P. 16150 in the British Museum. × $\frac{2}{3}$ diam.

The cephalic shield as a whole is strikingly narrow in proportion to its length. Its rostral part is pointed, but shows no clear evidence of any rostral process, and as the margin is imperfect it is impossible to say whether a rostral angle was present or not, but it seems very likely that it was. The cornua project slightly laterally and seem to have been slender. Their length cannot be measured, but it is obvious that it must have been equal to a third or a quarter of the distance from their tips to the supposed rostral angle. The inner margins of the cornua were probably destitute of denticles. The pectoral sinuses are well defined but seem to have been very shallow. The inter-zonal part is short and its breadth was approximately one-half of the maximum breadth of the shield. It is provided with a somewhat high dorsal spine, which, unlike those in *C. lankesteri* and *C. fletti,* is nearly vertical in position. The orbital openings, which are oval in shape and of medium size, are situated about midway between the rostral angle and the posterior end of the inter-zonal part. As in *C. lyelli,* the distance from their centres to the anterior end of the pectoral sinuses is much less than the distance from their centres to the supposed rostral angle. The dorsal electric field is about three times as long as broad and in general shape it seems to have been very much as in *C. lyelli.* The lateral electric fields are well developed and reach fairly far backwards on to the cornua.

The endoskeleton is entirely unknown, and the exoskeleton is in such an imperfect state of preservation that nothing can be learnt of its details.

Remarks.—*C. websteri* is in most of its known characters very suggestive of *C. lyelli.* However, it differs distinctly from that species by the more pointed rostral part of the cephalic shield and by the presence of the fairly high, vertical dorsal spine on the inter-zonal part. It has been named in honour of Mr. A. S. Webster, of the Albert Institute, Dundee.

It may be pointed out here that among the material of the Royal Scottish Museum in Edinburgh there is a cephalic shield (no. 1891.92.135) in a bad state of preservation, which has the rostral part pointed in a similar way to that of *C. websteri* and which shows remains of a dorsal spine. As this shield lacks the cornua and is distorted, it is not certain whether it belongs to *C. websteri* or represents an allied species.

Geological Formation and Locality.—Lower Old Red Sandstone: Locality uncertain (the matrix resembles those of Brechin, Kinblythmont, etc., Forfarshire).

17. *Cephalaspis langi*, sp. nov.

(Text-fig. 47; Pl. 14, figs. 1–4.)

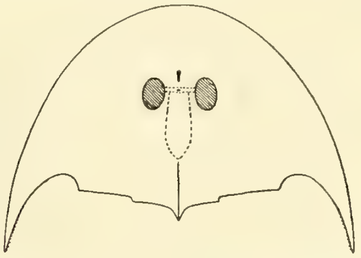
Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across distal ends of cornua, almost twice as great as length of cephalic shield in median line. Rostral part of cephalic shield broad and rounded without any evidence of rostral angle. Cornua projecting slightly laterally; their length constituting about one-third of distance of their tips from rostral end of cephalic shield; inner margins of cornua probably with small, forwardly inclined denticles. Pectoral sinuses rather narrow. Inter-zonal part short and broad, with low, backwardly inclined dorsal spine. Orbital openings fairly large and situated in front of middle of length of shield. Dorsal electric field about two and a half times as long as broad. Exoskeleton with (?) continuous superficial layer, which is smooth except on ventral rim, being there ornamented with numerous, small, obtuse tubercles. Mucous canal system enclosed in exoskeleton and forming uniformly fine-meshed network.

Holotype.—Cephalic shield with anterior part of associated trunk, in Ludlow Museum (no. E/a/20.I), Pl. 14, fig. 2.

Material.—This species is at present represented with certainty by two specimens only, both of which belong to the Ludlow Museum (the holotype and no. E/a/20.II). In addition to these I place here also, but with some hesitation, one other specimen which is in the British Museum (no. 46878).

The two specimens in the Ludlow Museum both consist of fragmentary cephalic shields associated with the anterior part of the scale-covered division of the trunk, whereas the British Museum specimen is an isolated cephalic shield only.

Description.—The cephalic shield of the holotype has the following dimensions: the length from the rostral margin to the posterior end of the inter-zonal part is about 2·7 cm.; the maximum breadth, which is between the posterior parts of the cornua, may be estimated at 4·5 cm. or slightly more; the maximum height, in the posterior half of the inter-zonal part, is about 1·3 cm. and it is thus great in proportion to the length of the shield; the distance from the tips of the cornua to the rostral end of the shield amounts to about 4 cm. Thus the cephalic shield of the holotype is fairly small. The cephalic shields of the other two specimens, though somewhat larger than that of the holotype, are both also small.



Text-fig. 47.—*Cephalaspis langi*, sp. nov. Cephalic shield in dorsal view. Mainly after the holotype, specimen no. E/a/20.I in Ludlow Museum. Nat. size.

A very characteristic feature of the cephalic shield of this species is its great relative breadth and the obtuseness of the rostral margin, which is rounded, without any evidence of a rostral angle. The cornua, which project somewhat laterally, are fairly long, their length equalling about one-third of the distance from their tips to the rostral end of the shield. In the holotype they are in a very poor state of preservation, but in the other two specimens their inner margins are provided with small, conical and forwardly-inclined denticles. The pectoral sinuses are well defined but not particularly broad. The inter-zonal part is fairly broad with a median dorsal crest, produced into a small, low dorsal spine, which is inclined backwards. The orbital openings are fairly large and lie in front of the middle of the length of shield. The dorsal electric field is probably about two and a half times as long as broad. The lateral electric fields are not sufficiently well preserved to show their extent backwards on to the cornua.

The endoskeleton of the cephalic shield is imperfectly preserved. In the holotype, however, impressions are to be seen of a few of the branchial fossae and also remains of the perichondrial bone-layers of some of the canals of the nerves of the lateral electric fields and of the sub-aponeurotic (sub-cutaneous) vascular plexus.

The exoskeleton of the cephalic shield is in such a very poor state of preservation that its details are difficult to make out. It is fairly obvious, however, that the superficial layer formed a continuous covering to the middle one. In the holotype, as well as in the other specimen in the Ludlow Museum, the exoskeleton of the cephalic shield is smooth except on the ventral rim, where it is apparently ornamented by numerous, very fine, blunt tubercles. In the British Museum specimen the ornamentation of the exoskeleton of the cephalic shield is preserved on the ventral rim only, where it is found to consist of numerous small tubercles, most of which are very obtuse.

The mucous canal system is enclosed in the exoskeleton and developed throughout as a fairly uniform, fine-meshed plexus in which the inter- and intra-areal canals cannot be clearly distinguished from one another.

The anterior part of the scale-covered division of the trunk, which in the two specimens in the Ludlow Museum is preserved in association with the cephalic shield, seems to have been of the usual shape. The scales are developed in the normal way but are strikingly narrow. As far as can be seen, they are provided with a continuous superficial layer, which is smooth and without any evidence of tubercles. The intra-areal canals are entirely enclosed in the scales.

REMARKS.—The specimens described here are very suggestive of *C. heightingtonensis*, but as they differ from this by their greater size, the greater breadth of the cephalic shield and the more oblique direction of the cornua, it is clear that they cannot be placed in that species, nor can they be referred to any other hitherto described. This new species has been named in honour of the curator of the Ludlow Museum, Dr. J. GILES LANG.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: near Pontrilas and (?) Cradley, Herefordshire.

18. *Cephalaspis watsoni*, sp. nov.

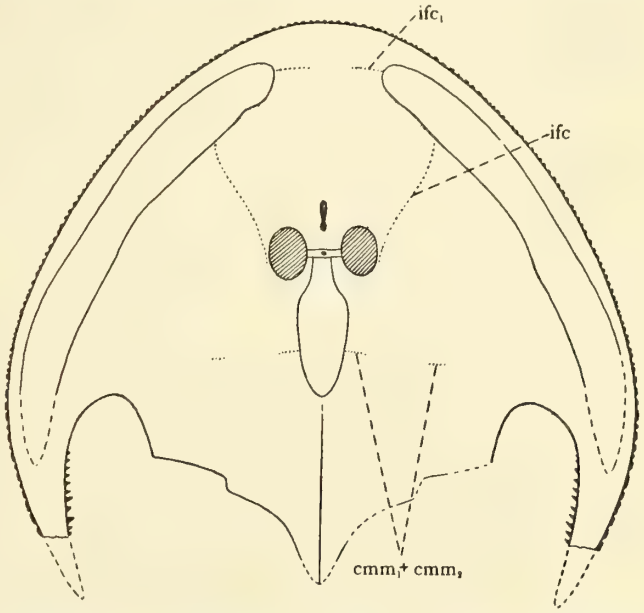
(Text-fig. 48; Pl. 19, figs. 3, 4.)

DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across bases of cornua, somewhat greater than length of cephalic shield in median line. Rostral part of cephalic shield rather broad anteriorly and without distinct rostral angle. Cornua projecting posteriorly but strongly curved inwards; their length contained between three and three and a half times in distance of their tips from rostral end of cephalic shield; inner margins of cornua with rather strong, forwardly-curved denticles. Pectoral sinuses deep but narrow. Inter-zonal part somewhat long, rather broad and with low, backwardly inclined dorsal spine. Orbital openings situated somewhat in front of middle of length of cephalic shield. Dorsal electric field about three times as long as broad with anterior third strikingly narrow. Lateral electric fields reaching backwards on to cornua. Exoskeleton with discontinuous superficial layer. Ornamentation consisting of tubercles, often somewhat recurved; tubercles smaller and obtuse along rostral and lateral margins and on ventral rim of shield. Mucous canal system situated more or less superficially to exoskeleton.

HOLOTYPE.—Impression of dorsal side of cephalic shield, in the Museum of Practical Geology, London (no. 47786), Pl. 19, fig. 4.

MATERIAL.—The material which I place in this species consists of three specimens, two of which belong to the Museum of Practical Geology, London (the holotype and no. 47788), and one to the British Museum (no. P. 16157). Two of the specimens (the holotype and the British Museum specimen) are represented by imperfect impressions of the dorsal side of the cephalic shield only, whereas the remaining one consists of the posterior half of a cephalic shield preserved in part as impression of the lower side.

Description.—All three specimens seem to have been of about the same size. The cephalic shield is about 6 cm. long from the rostral margin to the posterior end of the inter-zonal part, and between 7 and 8 cm. broad at the maximum, which is situated across the bases of the cornua or slightly further forwards. Since the shield in all the specimens is much flattened dorso-ventrally by pressure its present height is small, certainly much less than originally. The distance from the tips of the cornua to the rostral end of the cephalic shield is in the holotype about 7 cm., and it was probably about the same in the other two specimens, so that the species was of moderate size.



Text-fig. 48.—*Cephalaspis watsoni*, sp. nov. Cephalic shield in dorsal view. Chiefly after the holotype, specimen no. 47786 in the Museum of Practical Geology, London. Ornamentation omitted. Slightly enlarged. For explanation of lettering see text-fig. 23.

The cephalic shield is rather obtuse anteriorly and its rostral margin is destitute of a distinct rostral angle. The cornua, which project straight behind, are rather slender and curve very strongly inwards. Their length is contained slightly more than three times, perhaps even three and a third times, in the distance from their tips to the rostral end of the shield. On their inner margins they are provided with fairly well developed, conical denticles, which are curved forwards, and along their outer margin they bear, at least most posteriorly, enlarged obtuse tubercles belonging to the marginal series, which continues in front of the cornua. The pectoral sinuses are well defined and deep, but narrow. The inter-zonal part, although not particularly long, is nevertheless considerably longer than in *C. powriei*, *C. pagei* and most of the other British species of *Cephalaspis*. Its breadth at its hinder end is equal to somewhat more than one-half the maximum breadth of the shield, and dorsally it bears a median crest, which is produced into a low, backwardly inclined dorsal spine. The orbital openings, which are of moderate size, are situated somewhat in front of the middle of the length of the shield. The dorsal electric field is on the whole rather narrow, its maximum breadth constituting only about a third of the length, and it has a very characteristic shape, for its anterior part, comprising about one-third of its total length, is much narrower than the rest. In *C. powriei* and *C. pagei*, as well as in most other forms, the dorsal field also narrows somewhat forwards but not nearly so much nor so suddenly.

The lateral electric fields have their normal shape and reach backwards on to the cornua for a fair distance.

The endoskeleton of the cephalic shield is in part moderately well preserved in one of the specimens in the Museum of Practical Geology (no. 47788), for in this specimen we find considerable remains of the external perichondrial bone-layer, which must therefore have been at least tolerably well developed.

The exoskeleton of the cephalic shield is preserved almost entirely as an impression, but despite this it is quite evident that its superficial layer was not continuous. It is ornamented with numerous closely and irregularly set tubercles. On the dorsal side of the shield the tubercles are somewhat elongated and pointed, with the apices probably somewhat recurved. On the ventral rim and on the ventral sides of the cornua the tubercles are smaller, more numerous and probably more obtuse than on the dorsal side. Finally, on the rostral and lateral margins the tubercles are more irregular in shape than elsewhere, and are also somewhat enlarged, especially on the cornua, where they approach in relative size similarly placed tubercles in *C. pagei* and *C. powriei.*

The mucous canal system was not enclosed in the exoskeleton but was situated dorsally to it. In one of the unfigured specimens there are shallow grooves for the inter-areal canals, which were fairly thick and not subdivided. In the holotype, on the other hand, no distinct grooves are to be seen for either the inter- or intra-areal canals.

Some of the sensory canal grooves are fairly distinctly preserved (text-fig. 48).

Remarks.—The specimens described here have several characters in common with both *C. pagei* and *C. powriei,* and they are probably rather closely related to them. From *C. pagei* they differ by the greater breadth and the more obtuse shape of the anterior part of the cephalic shield, the direction and strong curvature of the cornua, the smaller orbital openings and by the shape of the dorsal electric field. From *C. powriei* and its varieties they differ by the more slender shape, direction and curvature of the cornua, by the length, shape and curvature of the denticles of the inner margins of the cornua, by the much deeper pectoral sinuses, the much longer inter-zonal part, the larger orbital openings and by the shape of the dorsal electric field. They are also suggestive of *C. arcticus* Stensiö, from the Downtonian of Spitsbergen, but they differ clearly from that species by their shorter cornua, stronger denticles on the inner margins of the cornua, narrower pectoral sinuses and by the very differently shaped dorsal electric field. It thus seems certain that they cannot be referred to any of the known species of *Cephalaspis,* but represent a new form. This new species I have named in honour of Professor D. M. S. Watson, of University College, London, to whom I am much indebted for valuable help in my work on the British Cephalaspids.

Geological Formation and Locality.—Lower Old Red Sandstone: Rossie Priory, Perthshire. (The locality of the specimen in the British Museum is uncertain, but it is probably also Rossie Priory.)

19. *Cephalaspis sollasi*, sp. nov.

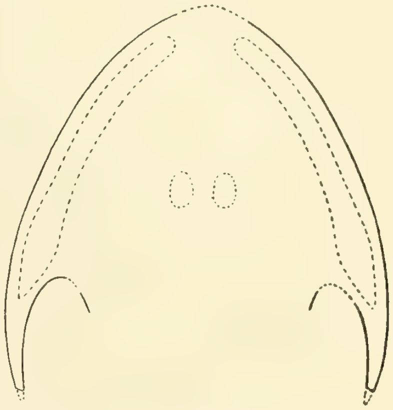
(Text-fig. 49; Pl. 25, fig. 2.)

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across anterior or middle parts of cornua, probably scarcely exceeding length of cephalic shield in median line. Rostral part of cephalic shield rather narrow. Cornua projecting directly backwards and curved somewhat inwards, slender and rather short, their length contained about three and a half times in distance of their tips from rostral end of cephalic shield; inner margins of cornua without denticles. Pectoral sinuses narrow. Inter-zonal part short and broad. Orbital openings situated about middle of length of cephalic shield, but nearer to pectoral sinuses than to rostral end of cephalic shield. Lateral electric fields probably reaching only slightly backwards on to cornua. Exoskeleton presumably with a continuous superficial layer. Ornamentation on the ventral surface of the cephalic shield consisting of slightly elongated, concentrically arranged tubercles.

Holotype.—Cephalic shield, in the University Museum, Oxford (not numbered), Pl. 25, fig. 2.

Material.—The holotype only, which is fragmentary and worn.

Description.—The length of the shield from the rostral angle to the posterior end of the inter-zonal part cannot be directly measured, as the most postero-dorsal portion of the inter-zonal part is wanting, but it may be estimated at about 8 cm. The maximum breadth, which seems to have been across the anterior parts of the cornua, was about 9 cm. The maximum height cannot be exactly determined, but it was probably about 2·5 cm., without the dorsal spine, if any. The distance from the tips of the cornua to the rostral end of the shield is almost 10·5 cm., and the breadth of the inter-zonal part at the hinder end approximately 5·3 cm.



Text-fig. 49.—*Cephalaspis sollasi*, sp. nov. Cephalic shield in dorsal view. After the holotype, in the University Museum, Oxford. × ½ diam.

As is seen from these measurements, the shield in question is from an individual of fairly large size.

Taken as a whole the shield is rather narrow in proportion to its length. Its most anterior part is wanting, and so it is impossible to decide whether a rostral angle was developed or not. The cornua project almost directly backwards, and are strikingly slender, but not particularly long, their length being contained not less than three and a half times in the distance from their tips to the rostral end of the shield. They are slightly curved inwards and their inner margins are without denticles. The pectoral sinuses are well defined but fairly narrow. The inter-zonal part is short, and its breadth posteriorly is somewhat greater than one-half the maximum breadth of the shield. It is imperfect dorsally, so that one cannot say if it bore a dorsal spine. The orbital openings seem to have been situated about midway between the rostral end and the postero-dorsal end of the inter-zonal part, but nevertheless they lie much nearer the pectoral sinuses than the rostral end, very much as in *C. lyelli* and *C. websteri*. The dorsal electric field is not preserved. The lateral electric fields are in a very imperfect state of preservation, but show that they reach only a fairly short distance backwards on to the cornua.

Of the endoskeleton we find in the shield several canal layers and traces of the orbital layer.

The exoskeleton of the cephalic shield is preserved only on the left cornu and on the ventral margin of the shield. It seems likely that its superficial layer was continuous. The ornamentation of the exoskeleton of the shield, at least on the ventral rim and on the ventral sides of the cornua, consists of numerous, very small tubercles, which are usually slightly elongated and arranged for the most part concentrically with the borders of the shield.

Of the mucous canal system nothing can be seen.

REMARKS.—This shield resembles somewhat in a few of its characters that of *C. salweyi*. It differs, however, distinctly from that by the shorter cornua, the narrower pectoral sinuses, the more posterior position of the orbital openings and the much finer tuberculation. As it cannot be referred to any of the other known forms, I have established for it a new species, which I have named in honour of Professor W. J. SOLLAS, of Oxford.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone : Cradley, Herefordshire.

20. *Cephalaspis woodwardi*, sp. nov.

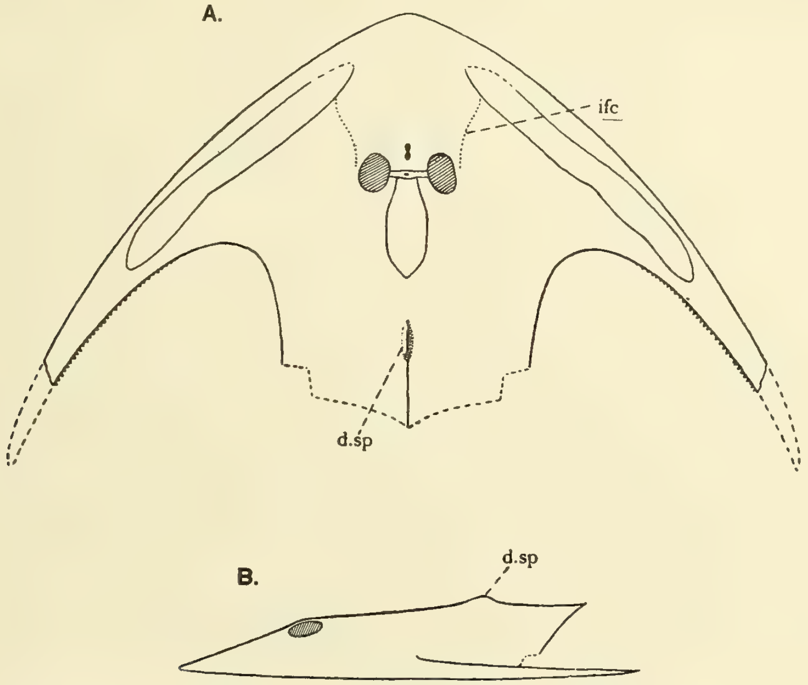
(Text-fig. 50; Pl. 20, figs. 1, 2.)

DIAGNOSIS.—A *Cephalaspis* with maximum breadth of cephalic shield, measured across posterior parts of cornua, almost twice as great as length of cephalic shield in median line. Rostral angle developed. Cornua projecting postero-laterally, slender and very long, their length being contained about twice in distance of their tips from rostral angle; inner margins of cornua with small, almost straight denticles. Pectoral sinuses very wide and deep. Inter-zonal part very long and narrow, its breadth constituting less than one-third of maximum breadth of cephalic shield; low, tubercle-like dorsal spine present anteriorly on inter-zonal part. Orbital openings situated considerably in front of middle of length of cephalic shield. Dorsal electric field about twice as long as broad. Lateral electric fields reaching backwards on to cornua. Exoskeleton with discontinuous superficial layer. Ornamentation consisting of one large central tubercle surrounded by several small peripheral tubercles on each polygonal area. Mucous canal system situated superficially to exoskeleton.

HOLOTYPE.—Cephalic shield, in the Museum of Practical Geology, London (no. 47789), Pl. 20, fig. 1.

MATERIAL.—The known material of this species consists only of two imperfect cephalic shields, both of which belong to the Museum of Practical Geology, London (the holotype and no. 47791). The more complete specimen, the holotype, lacks only the distal ends of the cornua and a small portion of the posterior end of the inter-zonal part; but the other is represented only by the exoskeleton of the dorsal side of the left half of the shield with its cornu.

Description.—The holotype has the following dimensions: the length of the cephalic shield from the rostral angle to the posterior margin of the inter-zonal part, as preserved, is 4·85 cm.; the maximum breadth, measured between the tips of the cornua, can only be estimated, since these parts of the cornua are missing; it was probably about 9 cm., that is, almost twice the length. The maximum height, which is situated in the inter-zonal part, is not more than 1 cm., and is thus extremely small compared with the length and maximum breadth, so that the shield as a whole is rather flat. The inter-zonal part is about 2·6 cm. broad at its posterior end. The other shield is only slightly larger than the holotype, so that both specimens are of moderate size.



Text-fig. 50.—*Cephalaspis woodwardi*, sp. nov. Cephalic shield. A, dorsal view; B, lateral view. After specimens nos. 47789 (the holotype) and 47781 in the Museum of Practical Geology, London. Slightly enlarged. *ifc*, infra-orbital sensory canal groove; *d.sp*, dorsal spine.

The rostral margin of the shield forms a distinct, though very obtuse, rostral angle. The cornua, which project postero-laterally, are slender and long in proportion to the size of the shield, their length being equal to not less than one-half of the distance from their tips to the rostral angle. Their inner margins are provided with small, tubercle-like denticles, which are almost straight. No distinct pectoral angles are present. The pectoral sinuses are wide and very deep. The inter-zonal part, the exoskeleton of which is closed ventrally, is strikingly long, its length being almost one-half the total length of the cephalic shield; and it has on its dorsal side a distinct dorsal median crest, which in its anterior half is produced into a low, and not very distinct dorsal spine. The orbital openings are of moderate size and situated considerably in front of the middle of the length of the shield, and they are longer than broad in both the specimens. The dorsal electric field, which is about twice as long as broad, does not reach backwards to the middle point between the pineal opening and the posterior margin of the inter-zonal part, while the lateral electric fields continue backwards for a short distance on to the proximal parts of the cornua.

Fragments of the endoskeleton are preserved in the holotype, and these show that the canals for the nerves of the lateral electric fields, both in number and arrangement, were typically *Cephalaspis*-like.

The exoskeleton is well developed, but the superficial layer is not continuous. The ornamentation is tubercular; on the dorsal side of the shield there is in the middle of each polygonal area a fairly large tubercle surrounded by a number of fairly small tubercles, the exact shape of which cannot be ascertained. On the ventral rim, and along the rostral and lateral margins of the shield, the ornamentation consists probably exclusively of numerous, small, obtuse tubercles.

The mucous canal system probably lay completely outside the exoskeleton, but nothing else is known about its development. The polygonal areas are numerous and very small in proportion to the size of the shield.

Remarks.—*C. woodwardi* is very well characterized as a species by the general shape of its cephalic shield, by the direction, shape and great length of the cornua, the great width and depth of the pectoral sinuses, the great length of the inter-zonal part and by the development of the ornamentation. It is named in honour of Sir A. Smith Woodward.

Geological Formation and Locality.—Lower Old Red Sandstone: Asylum Grounds, Abergavenny, Monmouthshire.

21. *Cephalaspis magnifica* Traquair.

(Text-fig. 51.)

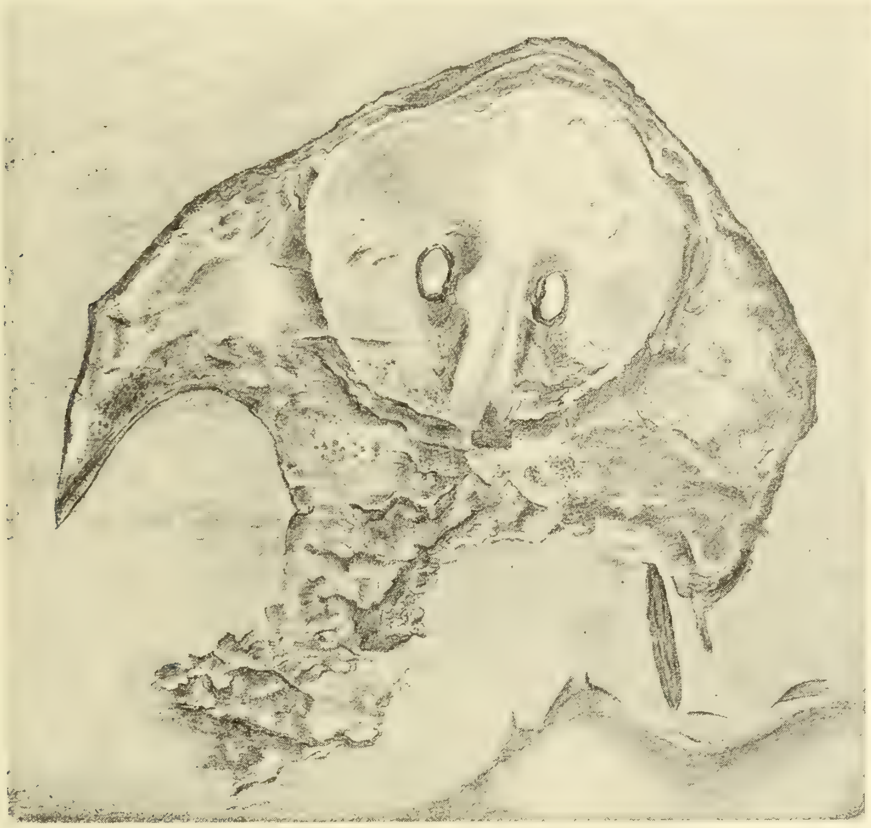
1893. *Cephalaspis magnifica*, R. H. Traquair, p. 206.
1894. *Cephalaspis magnifica*, R. H. Traquair, p. 270, pl. vii.

Diagnosis.—A *Cephalaspis* with maximum breadth of cephalic shield, measured approximately at base of cornua, about one and a half times as great as length of cephalic shield in median line. Rostral angle obtusely rounded. Cornua projecting slightly laterally, broad and probably rather short, their length contained about three or three and a half times in distance of their tips from rostral angle; inner margins of cornua without denticles. Pectoral sinuses broad and well developed. Inter-zonal part fairly long and narrow. Polygonal areas very small in proportion to size of cephalic shield. Ornamentation consisting of extremely small tubercles, somewhat coarser along margins of shield and around orbits than elsewhere.

Holotype.—Cephalic shield with parts of associated squamation, in the Royal Scottish Museum, Edinburgh (specimen described and figured by Traquair, 1894, p. 270, pl. vii).

Material.—The material of this species consists of a single specimen, the holotype. As this specimen could not be sent to me in Stockholm on account of its fragility, I have not had the opportunity of studying it, and the account given below is entirely based on the description given by Traquair in 1894 (see text-fig. 51).

Description.—The cephalic shield is very large, in fact, one of the largest known. The maximum breadth of the shield in its present completely flattened state was estimated by Traquair at about 30 cm., and its length from the rostral end to the posterior end of the inter-zonal part about 20 cm. or slightly more.



Text-fig. 51.—*Cephalaspis magnifica* Traquair. The holotype, a cephalic shield in ventral view. After Traquair 1894. × ⅓ diam.

The rostral margin has a distinct though blunt rostral angle. From this angle the rostral margin continues straight postero-laterally, to merge into the lateral margin, which is also quite straight for some distance before it turns to run almost directly backwards; the outlines of the shield are thus very characteristic. The cornua, which project slightly laterally, are perhaps not preserved in their entirety, but it is obvious that they were broad and flat. According to Traquair's statements they have no denticles on the inner margins. The pectoral sinuses are well defined and broad. The inter-zonal part is imperfectly preserved, but as far as can be seen it was fairly long. Its exoskeleton is closed ventrally, *i.e.* is not represented there by isolated scales in the middle of the underside, as in *Hemicyclaspis*, but is continuous as is normally the case in species of *Cephalaspis*. The orbital openings, which are oval in shape, seem to be situated about midway between the rostral angle and the posterior end of the inter-zonal part as preserved, but somewhat nearer to the anterior end of the pectoral sinuses than to the rostral angle. The electric fields are not to be seen. The oralo-branchial fenestra is well exposed, and in its present state of preservation more or less circular in outline.

The exoskeleton is imperfectly known in detail. Whether the superficial layer was continuous or not cannot be decided from the account given by TRAQUAIR, who describes the ornamentation as consisting of excessively minute tubercles, which are, however, coarser along the margins of the shield, near the orbits, and along the inner margins of the cornua.

The mucous canal system is not described by TRAQUAIR, who, however, noticed the polygonal areas and called attention to the fact that these were very small in proportion to the size of the shield.

Fragments of the squamation associated with the cephalic shield show that the scales had a similar tubercular ornamentation.

REMARKS.—*C. magnifica* is easily distinguished from all other species known as yet by the large size and configuration of its cephalic shield.

In shape its cephalic shield resembles somewhat those of *C. jexi* and *C. laticeps* from Canada, and *C. borealis*, *C. laticornis*, *C. lata* and *C. hoegi* from Spitsbergen.

GEOLOGICAL FORMATION AND LOCALITY.—Middle Old Red Sandstone: Spital, Caithness.

22, 23. *Cephalaspis* spp. nov.?

No. 1.

(Text-fig. 52; Pl. 18, fig. 1.)

MATERIAL.—A single, imperfectly preserved cephalic shield in the British Museum (no. 45946).

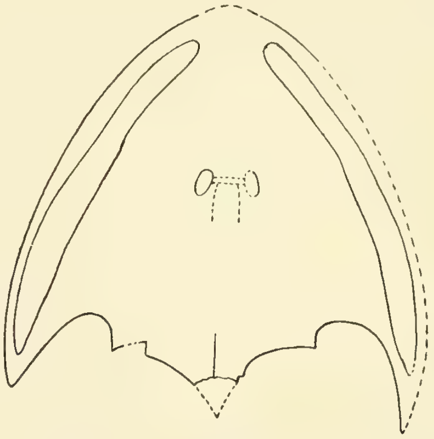
DESCRIPTION.—The cephalic shield measures in length about 6·2 cm. from the rostral end to the posterior margin of the inter-zonal part as now preserved. Its maximum breadth, which seems to have been across the middle or posterior parts of the cornua, is about 7 cm. Its maximum height, as usual at the hinder end of the inter-zonal part, is about 2 cm. excluding the dorsal spine, if present. The distance from the posterior end of the right cornu to the rostral end of the shield is about 8 cm., whereas that from the posterior end of the left cornu is only 7·3 cm., the left cornu being shorter than the right. The inter-zonal part is 3·3 cm. broad posteriorly.

The rostral part of the shield is narrow, but despite this the extremity seems to have been rather obtuse. As the margin here is imperfectly preserved, it is impossible to be sure whether a rostral angle was present or not. The cornua project slightly laterally and both are fairly short, but, as noted above, the left cornu is considerably shorter and broader than the right. Apparently this discrepancy in length between the two is not due to *post mortem* distortion, but to malformation in life. The length of the right cornu is contained three and a half to three and three-quarter times in the distance from its tip to the rostral end of the cephalic shield. Both cornua are slightly curved inwards, the right, however, somewhat more than the left. Their inner margins bear no denticles. The pectoral sinuses are well defined but fairly narrow. The inter-zonal part is short, and it seems not unlikely that it was provided with a low dorsal spine. The orbital openings, which are oval in shape and notably small, are situated somewhat in front of the middle point between the present posterior margin of the inter-zonal part and the rostral end of the shield. The dorsal electric field is very imperfectly preserved and its shape cannot be determined. The lateral electric fields reach rather far backwards on to the cornua. Some of the anterior plates covering the left lateral electric field are preserved, and one is strikingly large.

The endoskeleton is partly ossified, and parts of the orbital and labyrinth bone-layers and several canal layers are to be observed.

The exoskeleton is provided with a continuous superficial layer, which at least on the ventral rim and on the margins and ventral sides of the cornua is without tubercles.

The mucous canal system is situated entirely within the exoskeleton, and it is throughout developed as a fine-meshed plexus in which the inter-areal canals do not seem to be distinguishable.



Text-fig. 52.—*Cephalaspis* sp. nov.? Cephalic shield in dorsal view. After specimen no. 48946 in the British Museum. × $\frac{4}{5}$ diam.

Remarks.—This cephalic shield resembles in some respects those of *C. lankesteri*, *C. fletti*, *C. cradleyensis* and *C. whitbachensis*, but it differs in many characters from them, and, indeed, from those of all other known species. Since it is irregular in the development of the cornua, it is not improbable that it may be aberrant in other respects also, and thus it does not necessarily represent a new species, but may belong to one of the species mentioned above. On this account I thought it best for the present to describe it merely as a possible new species without naming it.

Geological Formation and Locality.—Lower Old Red Sandstone: Whitbach, Shropshire.

No. 2.

(Pl. 37, fig. 1.)

Material.—A single, imperfect cephalic shield which is somewhat distorted and compressed dorso-ventrally. It is in the British Museum (specimen no. P. 3234).

Description.—The length of the shield from the rostral margin to the posterior end of the inter-zonal part cannot be determined exactly, but it seems to have been about 3·5 cm. or slightly more. The maximum breadth, which is across the middle of the cornua, is in the fossil 5·4 cm., but was probably somewhat less before the shield was affected by pressure. The distance from the tip of each cornu to the rostral end of the shield is about 5·6 cm. The breadth of the inter-zonal part at the hinder end is, in its present somewhat flattened condition, about 2·5 cm., but was probably originally a little less.

The rostral part of the shield is fairly narrow, but as the rostral margin is imperfectly preserved it is impossible to decide whether a rostral angle was present or not. The cornua project slightly laterally, and are in most respects very suggestive of those in *C. lyelli*: they are fairly broad and not much curved inwards, and their length seems to equal about a third of the distance from their tips to the rostral end of the shield; moreover, they also exhibit definite traces of a pectoral angle, just as in *C. lyelli*. But whereas on the cornua of *C. lyelli* I was unable to observe any denticles, those of the shield here under consideration bear a number of denticulations on their inner margins. The pectoral sinuses are well defined but not so very broad, and the inter-zonal part is short and fairly narrow. As its dorsal portion is wanting, it is impossible to say whether a dorsal spine was developed or not. The orbital openings are not preserved, but nevertheless it is clear that they must have been situated further forwards than in *C. lyelli*. The dorsal electric field is also destroyed. The lateral electric fields continue backwards on to the cornua for a short distance.

The endoskeleton of the shield is fairly well ossified, and remains are to be found of the following perichondrial bone-layers: the external, the orbital, the internal and those lining the canals of the nerves of the lateral electric fields.

The exoskeleton of the shield is so imperfectly preserved that it is impossible to decide whether its superficial layer was continuous or not. On the ventral rim, and on the ventral side of the cornua, it is ornamented with closely set, obtuse, elongated tubercles, which are arranged chiefly concentrically with the borders of the shield.

REMARKS.—This shield was referred by WOODWARD in 1891 (p. 180) to *C. lyelli*, and it cannot be denied that in several characters it is very suggestive of that species. However, it differs from *C. lyelli* in the characters noted above, which cannot very well have arisen from distortion or compression, and I do not therefore think it possible that it belongs to that species: and as it cannot be referred to any other known forms it seems probable that it represents a new species.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Glammis, Forfarshire.

zz. Indeterminable Specimens of CEPHALASPIS

Specimen no. 1891.92.182 in the Royal Scottish Museum, Edinburgh.

(Text-figs. 5H, 53; Pl. 24, figs. 1, 2.)

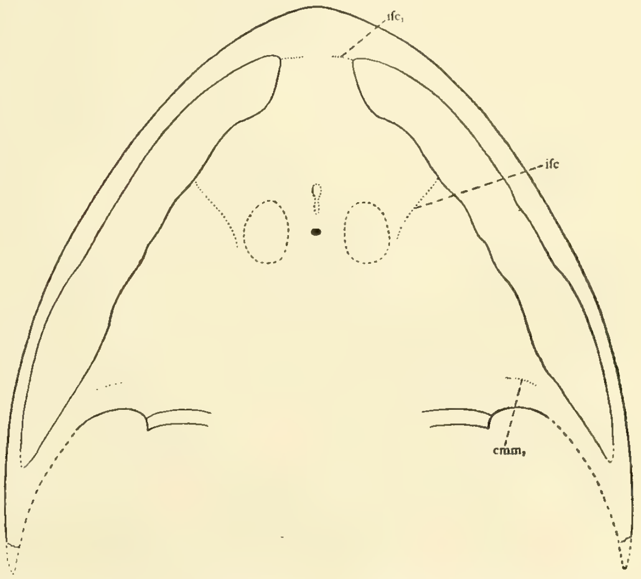
DESCRIPTION.—This specimen consists of an imperfect cephalic shield, which is displayed from the ventral side.

As the postero-dorsal portion of the inter-zonal part is wanting, the length of the shield from the rostral end to the posterior end of the inter-zonal part cannot be directly measured, but it was probably about 4 cm. The estimated maximum breadth across the middle or posterior parts of the cornua is about 5 cm. The maximum height, at the hinder end of the inter-zonal part, seems to be about 1·5 cm., excluding the dorsal spine, if present. The distance from the rostral end to the tips of the cornua was probably about 5·6 cm., and the breadth of the inter-zonal part at the posterior end seems to have been about 2·4 cm.

A rostral angle is present. The cornua, which project somewhat laterally, are rather imperfectly preserved, so that their exact length and breadth cannot be measured, nor is it possible to see if denticles were present along their inner margins. The pectoral sinuses are narrow and shallow, and the inter-zonal part short. The orbital openings, which are fairly large, seem to have been situated at the middle, or a little further forwards, of the length of the shield, measured from the rostral end to the posterior margin of the inter-zonal part. The dorsal electric field is not exposed. The lateral electric fields, which are rather broad, continue for some distance backwards on to the cornua.

The endoskeleton appears to have been strikingly well ossified, and both the labyrinth bone-layer and parts of the internal bone-layer are to be observed.

The exoskeleton is lined by a continuous superficial layer, which is smooth, without tuberculations.



TEXT-FIG. 53.—*Cephalaspis* sp. Cephalic shield in dorsal view. After specimen no. 1891.92.182 in the Royal Scottish Museum, Edinburgh. × $\frac{2}{3}$ diam. For explanation of lettering see text-fig. 23.

The mucous canal system is very well displayed, and it is obvious that it was entirely enclosed in the exoskeleton. Its detailed arrangement is well shown in fig. 2, Pl. 24, and as is seen from this figure, the inter-areal canals are fairly wide, not subdivided and very easily distinguishable from the intra-areal canals, which form a fairly wide-meshed plexus with one another. The polygonal areas are mostly small in proportion to the size of the cephalic shield.

Some of the lateral sensory canal grooves are to be observed on the shield.

REMARKS.—This cephalic shield was figured by LANKESTER in 1870 (Pl. 10, fig. 2), but was not determined by him. In general shape and proportions it is suggestive of *C. pagei*, but since it differs from that species by its broader and shallower pectoral sinuses, a shorter inter-zonal part, the absence of tuberculations, the much wider mesh of the intra-areal mucous canal plexus and by the generally less complicated development of the mucous canal system, it is obvious that it must belong to another species; but owing to its imperfect state of preservation, it is impossible to decide whether it belongs to any other known species of *Cephalaspis* or represents a new form.

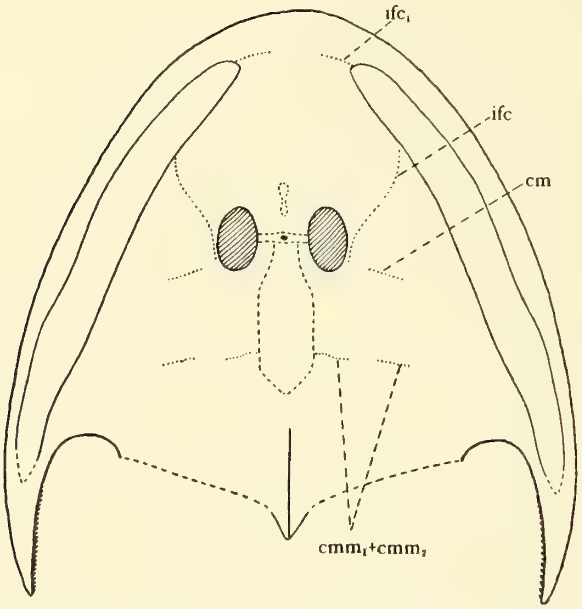
Geological Formation and Locality.—Lower Old Red Sandstone: Forfarshire.

Specimen no. P. 6954 in the British Museum and specimen no. 47813 in the Museum of Practical Geology, London.

(Text-fig. 54; Pl. 23, fig. 1; Pl. 56, fig. 3.)

Description.—Of these two specimens the first mentioned is a complete cephalic shield, which is much compressed laterally; whereas the other is an imperfect cephalic shield exposed from the ventral side. Both shields are of similar size. The length measured from the rostral end to the posterior end of the inter-zonal part is about 4 cm. The other dimensions, which can be ascertained only in the specimen belonging to the Museum of Practical Geology, are as follows: the maximum breadth, measured across the posterior parts of the cornua, is about 4·9 cm., and the maximum height about 1·4 cm., excluding the dorsal spine. The distance from the rostral end of the shield to the tips of the cornua is 5·4 cm. Finally, the breadth of the inter-zonal part at the hinder end may be estimated at about 2·9 cm.

The rostral margin of the shield is obtuse, without a distinct rostral angle. The cornua, which project only very slightly laterally, are rather slender and short, their length being contained somewhat more than three and a half times in the distance from their tips to the rostral end of the shield. Their inner margins are provided with small, forwardly curved denticles. The pectoral sinuses are shallow and probably fairly narrow. The inter-zonal part, which is rather short, is provided with a moderately low, backwardly inclined dorsal spine. The orbital openings are fairly large and situated somewhat in front of the middle of the length of the shield, measured from the rostral end to the posterior end of the inter-zonal part. The dorsal electric field, which is exposed only in the specimen in the Museum of Practical Geology, is almost three times as long as broad. Its shape is very characteristic, for its anterior third is much narrower than the remainder, and thus it is very suggestive of the dorsal field in *C. watsoni*. The lateral electric fields continue for a short distance backwards on to the cornua.



Text-fig. 54.—*Cephalaspis* sp. Cephalic shield in dorsal view. After specimen no. 47813 in the Museum of Practical Geology, London. × 1½ diam.
For explanation of lettering see text-fig. 23.

Of the endoskeleton, only a few of the canal layers are to be seen in the British Museum specimen.

The exoskeleton is well developed and provided with a continuous superficial layer, which, at least in the British Museum specimen, is entirely smooth.

The mucous canal system is enclosed in the exoskeleton. The inter-areal canals (*iac*, Pl. 56, fig. 3) are wide, and not subdivided, and are thus clearly distinguishable from the intra-areal canals (*ita*). The latter form, as usual, a fine-meshed intra-areal plexus. In the specimen belonging to the Museum of Practical Geology their arrangement varies somewhat in different parts of the shield : thus in the pre-nasal part they are arranged more or less concentrically with the inter-areal canal surrounding each polygonal area; whereas more posteriorly the longest and most conspicuous intra-areal canals in each polygonal area run chiefly longitudinally. In the British Museum specimen they are for the most part destroyed so that very little can be seen of their arrangement, but it seems that they were more irregularly arranged than in the specimen belonging to the Museum of Practical Geology.

Remarks.—The two cephalic shields described here are somewhat suggestive of *C. pagei* and *C. watsoni*, but since they differ from these two species in their general shape, the shorter and differently shaped cornua, the absence of tuberculations, the development of the mucous canal system and also in certain other characters they cannot be referred to either of those two species. As they are imperfect in many respects it is difficult to say whether they should be placed in any other species of *Cephalaspis* or whether they represent new forms. Under these circumstances I have considered it best to describe them here as indeterminable.

Geological Formation and Localities.—Lower Old Red Sandstone: Aberlemno and Sidlaw (*sic*), Forfarshire.

Specimen no. 1891.92.172 in the Royal Scottish Museum, Edinburgh, and its counterpart, specimen no. P. 16147 in the British Museum.

(Pl. 34.)

Description.—This specimen consists of the posterior part of the caudal region with the posterior dorsal and caudal fins.

The posterior dorsal fin (D_2, Pl. 34, fig. 1) is imperfectly preserved, but it is clearly seen that the scales covering its membrane are arranged in rows so as to form fairly distinct lepidotrichia.

The caudal fin, which is very well displayed, has a similar shape to those in *Hemicyclaspis murchisoni*, *Cephalaspis pagei* and *C. powriei*. The lobe supported by the ventral axis (*vhp*) is more or less independent, and its scales are arranged differently from those of the other lobes, of which the scales are, as in the posterior dorsal fin, arranged so as to form fairly distinct lepidotrichia.

The squamation is imperfectly preserved, but is on the whole like that in *C. pagei* and *C. powriei*. The most dorsal scales of the caudal fin, however, are developed differently; for immediately below the fulcral scales (dorsal ridge-scales) there are a few which are larger than the others on the main axis of the fin, but which seem to be rather variable in size and shape. These large scales are separated from the remainder on the dorsal axis by a longitudinal row of long, low scales.

Whether the scales had a continuous superficial layer it is impossible to decide. The ornamentation of the scales consists of tubercles, which seem to be considerably more delicate than in *C. pagei* or *C. powriei* and its varieties.

REMARKS.—The fragment of the scale-covered division of the trunk just described resembles the corresponding parts in *C. pagei* and *C. powriei*, but it seems to differ from these in the details of the squamation of the main axis of the caudal fin, and probably it cannot be referred to either of these species: indeed, it is too imperfect to say to what species it does belong.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Turin Hill, Forfarshire.

GENUS ATELEASPIS Traquair.

1899*b*. *Ateleaspis*, R. H. Traquair, p. 834.

DIAGNOSIS.—An imperfectly known Cephalaspid genus provisionally referred to the sub-family CEPHALASPINAE. Distinct head-shield probably present; head region rounded in front, produced postero-laterally into "lappet-like expansions" probably representing either cornua or pectoral fins, or both. Dorsal electric field well developed; lateral electric fields unknown. Trunk generally triangular in cross-section. Anterior dorsal fin absent; posterior dorsal fin situated far back, apparently without anterior spine. Caudal fin heterocercal. Squamation, as far as known, resembling that of *Cephalaspis*.

GENOTYPE.—*A. tessellata* TRAQUAIR.

REMARKS.—The above diagnosis is provisional and obviously unsatisfactory, but many of the features of this interesting form are uncertain owing to the bad state of preservation of the known specimens, and moreover, these I have not had the opportunity of studying.

This genus was founded and first described in 1899 by TRAQUAIR (1899*b*, pp. 834–837), who subsequently gave a more complete account of it on the basis of new and better preserved material (TRAQUAIR 1905, pp. 883–886).

In 1899 TRAQUAIR expressed the opinion that *Ateleaspis* represented a new family of Cephalaspids, a family which he called 'ATELEASPIDAE' (*cf.* also WOODWARD 1902, p. 54). In 1905, after studying the better preserved material then available, he placed *Ateleaspis* in the CEPHALASPIDAE, expressing himself as follows:—"Finally, as the general resemblance between *Ateleaspis* and *Cephalaspis* is now seen to be so close, I no longer see the necessity of allotting a distinct family to the former genus, and propose therefore to classify it henceforth as a member of the Cephalaspidae." Since then writers dealing with the Cephalaspids have generally accepted this last view (KOKEN 1911, p. 34; SCHLOSSER 1918, p. 34; 1923, pp. 34, 35; ABEL 1919, p. 77, etc.).

As no new material of *Ateleaspis* has been described since 1905 our knowledge of this genus is still very imperfect: we do not know for certain the configuration of the hinder margin of the cephalic shield, the lateral electric fields and the course and relations of their nerve-canals, and the course of the main vascular canals of the cephalic shield; while the development of the pectoral fins is still obscure. It is thus impossible to arrive at any more exact conclusions as to the precise relationships of *Ateleaspis* than those of TRAQUAIR in 1905, and accordingly *Ateleaspis* has here been retained in the family CEPHALASPIDAE. Since in the development of the dorsal electric field, the general shape of the trunk, the position and development of the posterior dorsal fin, and in the squamation it essentially agrees with *Hemicyclaspis* and *Cephalaspis*, and differs from *Thyestes*, it has here been placed provisionally in the sub-family CEPHALASPINAE.

We may at this point offer a few remarks on the exoskeleton of the cephalic shield of *Ateleaspis*. According to TRAQUAIR this exoskeleton was not continuous, as in the other Cephalaspids, but was represented by independent polygonal plates (tesserae). However, from TRAQUAIR'S descriptions and figures it is not difficult to see that in fact these ' tesserae ' are simply polygonal areas, according to the terminology employed in this work. These areas under certain conditions do have the appearance of independent plates, even in those forms in which the exoskeleton of the cephalic shield is beyond question continuous; and so one may at least strongly suspect that in *Ateleaspis* also the exoskeleton was of a similar nature, but that the bony tissue between its polygonal areas is always fractured and weathered (*cf.* Pl. 28, fig. 3; Pl. 30, fig. 3; Pl. 31; Pl. 38, figs. 3, 4; Pl. 39, fig. 1; Pl. 40, fig. 1; Pl. 43, fig. 2). Sclerotic rings seem to have been developed (*cf.* TRAQUAIR 1905, Pl. 2, fig. 9).

As noted above, the material of *Ateleaspis* described by TRAQUAIR has not been submitted to me for examination, and I have therefore no new facts of importance to add to previous observations, and do not propose to give here any further description of the only species, *A. tessellata* TRAQUAIR, which is from the Downtonian of Ayrshire and Lanarkshire (see also pp. 1, 4, 9, 10, 16, 54).

Sub-family *KIAERASPINAE*.

DIAGNOSIS.—Electric fields well developed in certain forms, fairly short in others. Lateral electric fields usually with postero-medial angle, strongly developed in some forms. Independent canals of two most anterior nerves of lateral electric fields short or absent, their common canal extending close to, or even into, lateral electric fields. Canal of n. trigeminus proper passing down to oralo-branchial chamber either entirely posteriorly, or entirely anteriorly, to canal or canals of two most anterior nerves of lateral electric fields. Canal of dorso-lateral superficial vein 3 usually opening into canal of post-orbital division of v. capitis lateralis.

GENERA.—*Benneviaspis* STENSIÖ, *Securiaspis* STENSIÖ, *Hoelaspis* STENSIÖ, *Boreaspis* STENSIÖ, *Kiaeraspis* STENSIÖ, *Thyestes* EICHWALD, *Didymaspis* LANKESTER and *Sclerodus* AGASSIZ [*Eukeraspis* LANKESTER].

REMARKS.—As pointed out in the general account of the family CEPHALASPIDAE (pp. 74–76) the sub-family KIAERASPINAE also differs from the CEPHALASPINAE by certain characters of the squamation and fins, but as these are very imperfectly known, they have not been taken into consideration either in the diagnosis of the KIAERASPINAE or in that of the CEPHALASPINAE.

In the sub-family KIAERASPINAE, as defined above, two groups of genera may be distinguished.

The first of these groups, which includes the genera *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis* and *Kiaeraspis*, is characterized as follows :—The electric fields are usually well developed, especially the lateral fields, which always begin as far forward as in the sub-family CEPHALASPINAE; the independent canals of the two most anterior nerves of each lateral electric field are either short or entirely absent, the common canal of these two nerves extending in the latter case right down to the field; the canal of the n. trigeminus proper passes down to the oralo-branchial chamber in the space between the common canal of the two most anterior nerves of the lateral electric fields and the canal of the third nerve.

The other group, to which *Thyestes, Didymaspis* and *Sclerodus* [*Eukeraspis*] are referred, is characterized thus :—The electric fields are always less strongly developed than in the other Cephalaspids; the dorsal field begins more or less close behind the pineal depression and ends close in front of, or at, the supposed canal of the ductus endolymphaticus; the lateral fields never begin so far forward as in the other Cephalaspids and never extend backwards on to the cornua, however strongly these are developed; the common canal of the two most anterior nerves of the lateral electric fields always reaches down to the fields without dividing into two independent canals, and not only the canal of the n. trigeminus proper, but also the canal of the n. facialis, passes down to the oralo-branchial chamber in front of this common canal, so that the course of the two anterior nerves of the lateral electric field was much more posterior in position in these than in any other Cephalaspids, a situation doubtless due to the lateral electric fields not extending nearly so far forwards in this group as in the others. In this respect the three genera in this group seem to approach *Tremataspis*, in which the most anterior nerve-canal of the anterior division of each lateral electric field also lies far back (*cf.* STENSIÖ 1927, Pl. 60).

It is very likely that when our knowledge of the Cephalaspids has become more extended, especially by the discovery of specimens with the scale-covered division of the trunk well preserved, it will be necessary to erect an independent sub-family for each of the above two groups of genera. In such a case we would, of course, have to confine the name KIAERASPINAE to the group comprising the genera *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis* and *Kiaeraspis*, whereas for the other group, comprising *Thyestes, Didymaspis* and *Sclerodus*, it would be necessary to introduce a new name.

GENUS BENNEVIASPIS Stensiö.

1927. *Benneviaspis*, E. A. Stensiö, p. 288.

DIAGNOSIS.—KIAERASPINAE with cephalic shield broad, depressed and roughly triangular in outline. Cornua fairly well developed, projecting much laterally but never extending backwards beyond posterior margin of inter-zonal part. Pectoral sinuses broad and usually fairly shallow. Inter-zonal part closed ventrally, rapidly decreasing in breadth backwards; its postero-lateral angles much produced, sometimes even extending further backwards than posterior angle. Dorsal electric field well developed and long. Lateral electric fields usually extending somewhat backwards on to cornua, and with marked postero-medial angles reaching on to zonal part in front of pectoral sinuses. Common canal of two most anterior nerves of lateral electric fields extending to point about midway between each orbital opening and lateral electric field. Canal of n. trigeminus proper running entirely behind canal or canals of two most anterior nerves of lateral electric fields. Canal of dorso-lateral superficial vein 3 opening into canal of v. capitis lateralis somewhat behind orbit. Middle layer of exoskeleton of cephalic shield with well-developed radiating canals.

Genotype.—*B. holtedahli* Stensiö.

Remarks.—When *Benneviaspis* was established in 1927 I pointed out that it was represented not only by the genotype, from Spitsbergen, but also by an English species, for which the name *B. lankesteri* was suggested. Among the material of Cephalaspids from England now at my disposal I have been able to distinguish in addition to *B. lankesteri* yet another species of *Benneviaspis*, *B. anglica*, so that three species of this genus are now known.

With regard to the geological range of *Benneviaspis*, it may be mentioned that *B. holtedahli* is known only from the Downtonian, whereas both *B. lankesteri* and *B. anglica* have as yet been found only in the Lower Old Red Sandstone.

As pointed out in my description in 1927, *Benneviaspis* belongs to the group of Cephalaspids comprising *Hoelaspis*, *Boreaspis* and *Kiaeraspis*, and it is certainly also related to the newly-established genus *Securiaspis* described below. On the other hand, it is not so closely akin to *Thyestes* as I formerly supposed: it is true that in the general shape of the cephalic shield it resembles *Thyestes*, but whereas in *Thyestes* the n. trigeminus proper ran down to the oralo-branchial chamber in front of all the nerves of the lateral electric fields, in Benneviaspis this nerve passed down between the second and third nerves, as in *Securiaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis*. In addition, *Benneviaspis* differs from *Thyestes* by the fact that the extent of the electric fields is similar to that in the Cephalaspinae.

1. *Benneviaspis lankesteri*, sp. nov.

(Text-figs. 11, 55; Pl. 47; Pl. 49, fig. 3.)

1891. *Cephalaspis lyelli* (in part), A. S. Woodward, p. 181 (specimen no. 46877).

1927. *Benneviaspis lankesteri* (in part—*nomen nudum*), E. A. Stensiö, p. 289 (not specimen no. 46568).

Diagnosis.—A *Benneviaspis* with maximum breadth of cephalic shield, measured across posterior ends of cornua, almost twice as great as length in median line. Rostral angle present though indistinct. Lateral angles developed between rostral and lateral margins of cephalic shield; lateral margins of shield straight or slightly concave. Cornua short, their length being contained about five times in distance of their tips from rostral angle. Inner margins of cornua without denticles. Pectoral sinuses broad and shallow. Inter-zonal part narrowing rapidly backwards. Dorsal electric field about twice as broad as long and broadest at one-third of length from rear. Lateral electric fields continuing only for short distance backwards on to cornua. Exoskeleton with continuous superficial layer. Dorsal surface of cephalic shield smooth; the lateral margins on ventral side of the cephalic shield ornamented with small, flat tubercles. Mucous canal system enclosed in exoskeleton and probably developed as uniform, fine-meshed network.

Holotype.—Cephalic shield, in the British Museum (no. 46877), text-fig. 11; Pl. 47, fig. 2.

Material.—The material comprises three imperfectly preserved cephalic shields, belonging to the British Museum (holotype), the Royal Scottish Museum, Edinburgh (no. 1890.6.29), and the Geol.-Pal. Museum of the University of Berlin.

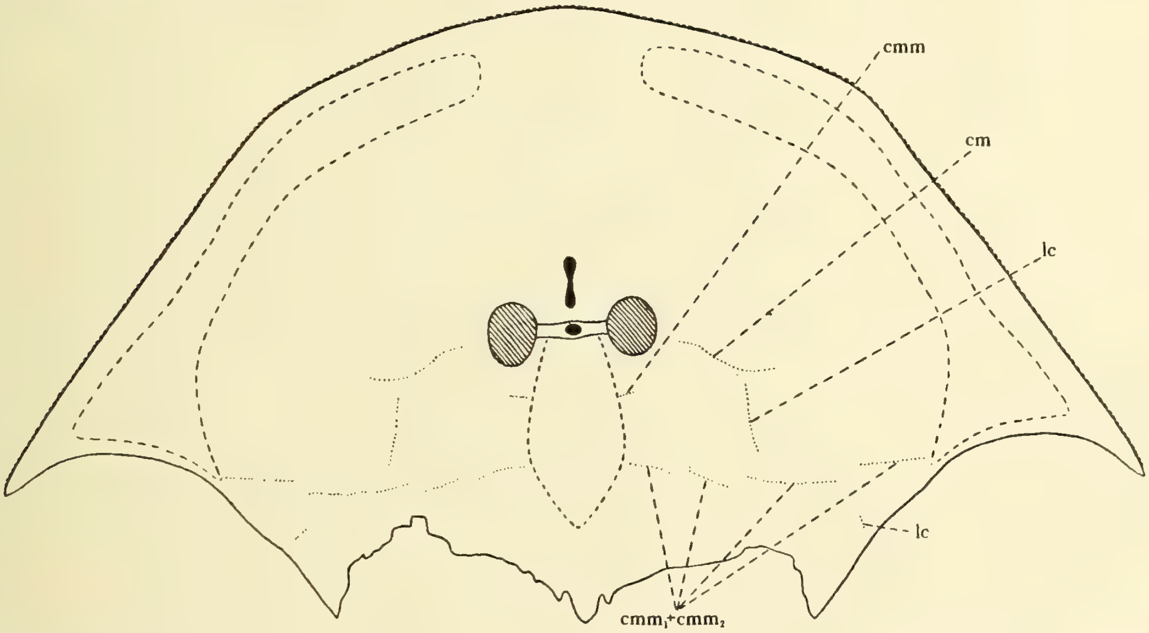
Description.—These shields seem to have been somewhat flattened, and are therefore a little lower and broader than they were in life. Their dimensions are as follows:

	Holotype.	R.S.M. no. 1890.6.29	Berlin specimen.
Length from rostral end to posterior end of inter-zonal part	3·4 cm.	3·3 cm.	3·5 cm.
Breadth across posterior ends of cornua (maximum breadth)	6·5 ,,	6·25 ,,	6·0 ,,
Height at posterior end of inter-zonal part (maximum height)	about 0·5 ,,	about 0·5 ,,	about 0·5 ,,
Distance from tip of cornu to rostral end of shield	4·0 ,,	4·0 ,,	4·0 ,,
Distance from postero-lateral angle to rostral end of shield	3·7 ,,	3·5 ,,	3·65 ,,
Breadth of inter-zonal part at posterior end	2·7 ,,	about 3·0 ,,	2·5 ,,

As will be seen from these measurements, all three shields are from small individuals of approximately equal size.

The rostral margin is obtusely rounded, with a faint indication of a rostral angle. At the transition between the rostral margin and each lateral margin there is an obtuse but fairly distinct angle. The lateral margins are not convex, as is usually the case in Cephalaspids, but either straight or slightly concave. The cornua, which project very obliquely, are strikingly short, their length constituting only about one-fifth of the distance from their tips to the rostral angle of the shield. They are flat and, as far as can be seen, bear no denticles on their inner margins. The pectoral sinuses are broad and shallow. The inter-zonal part, which projects for some distance behind the cornua, narrows rapidly backwards in a way typical of *Benneviaspis*. Its posterior angle is well developed and so are also its postero-lateral angles, which, as in the other species of the genus, reach even further backwards than the posterior angle. Between the posterior angle and each postero-lateral angle the posterior margin of the inter-zonal part is rather deeply concave.

The inter-zonal part has neither dorsal spine nor distinct dorsal median crest. The orbital openings, which are more or less oval in shape, are situated midway between the rostral and posterior angles of the shield, or slightly further to the rear. The dorsal electric field is short and broad, for its length is probably only twice as great as the maximum breadth. Its shape is characteristic, the maximum breadth being situated in the anterior part of the posterior half. The lateral electric fields, which are long and well developed, are as a whole somewhat broader than in *B. holtedahli*. Towards the posterior end each expands suddenly and becomes slightly forked, forming two angles, of which the outer projects for a very short distance on to the cornua, and the inner, and more acute, extends medially on to the zonal part in front of the pectoral sinus.



Text-fig. 55.—*Benneviaspis lankesteri*, sp. nov. Cephalic shield in dorsal view. Outlines after the holotype, specimen no. 46877 in the British Museum; sensory canal grooves after the Berlin specimen. Slightly more than × 2 diam. For explanation of lettering see text-fig. 23.

The endoskeleton of the cephalic shield seems to have been rather well ossified, but it is not well exposed.

The exoskeleton of the cephalic shield has a continuous superficial layer, which is smooth on the dorsal side of the shield, but provided with small, flat tubercles along the rostral and lateral margins, and probably also on the ventral rim and on the ventral surfaces of the cornua.

The mucous canal system of the cephalic shield is entirely enclosed in the exoskeleton. Its development is very imperfectly known, but it is most likely that it forms a uniform, fine-meshed plexus in which the inter- and intra-areal canals cannot be distinguished from each other.

The sensory canal grooves are well displayed in part in the Berlin specimen (see text-fig. 55).

Remarks.—This species, which is named in honour of the late Sir E. Ray Lankester, was mentioned, but not described, in my monograph of the Spitsbergen Cephalaspids (Stensiö 1927, p. 289). At that time I referred to it specimens nos. 46568 and 46877 in the British Museum. As, however, these two specimens now appear to be so different as to represent two distinct species, I have taken specimen no. 46877 as holotype of *B. lankesteri*, and for the other I have established a new species, *B. anglica* (see below).

B. lankesteri is well characterized as a species, as it differs both from *B. holtedahli* and *B. anglica* in several minor characters, especially in the shape and proportions of the whole shield, of the dorsal electric field, and the form and relative length of the cornua.

Geological Formation and Locality.—Lower Old Red Sandstone : Cradley, Herefordshire.

2. *Benneviaspis anglica*, sp. nov.

(Text-figs. 10, 56; Pl. 48, fig. 2.)

1891. *Cephalaspis lyelli* (in part), A. S. Woodward, p. 181 (specimens nos. 46568, 46569).
1927. *Benneviaspis lankesteri* (in part), E. A. Stensiö, p. 289 (specimen no. 46568).

Diagnosis.—A *Benneviaspis* with maximum breadth of cephalic shield, measured across posterior parts of cornua, about one and three-quarter times as great as length in median line. Rostral angle present though rather indistinct. Lateral angle developed between rostral and lateral margins of cephalic shield; lateral margins of cephalic shield distinctly concave. Cornua slender and rather long, their length being contained nearly four times in distance of their tips from rostral angle. Inner margins of cornua, at least posteriorly, with forwardly curved denticles. Pectoral sinuses broad and deep. Inter-zonal part narrowing moderately rapidly backwards. Dorsal electric field probably more than twice as long as broad. Lateral electric fields continuing for short distance backwards on to cornua. [Condition of superficial layer of exoskeleton unknown.] Ventral side and rostral and lateral margins of cephalic shield ornamented with numerous, small, flat tubercles.

Holotype.—Cephalic shield, in the British Museum (no. 46568), text-fig. 10; Pl. 48, fig. 2.

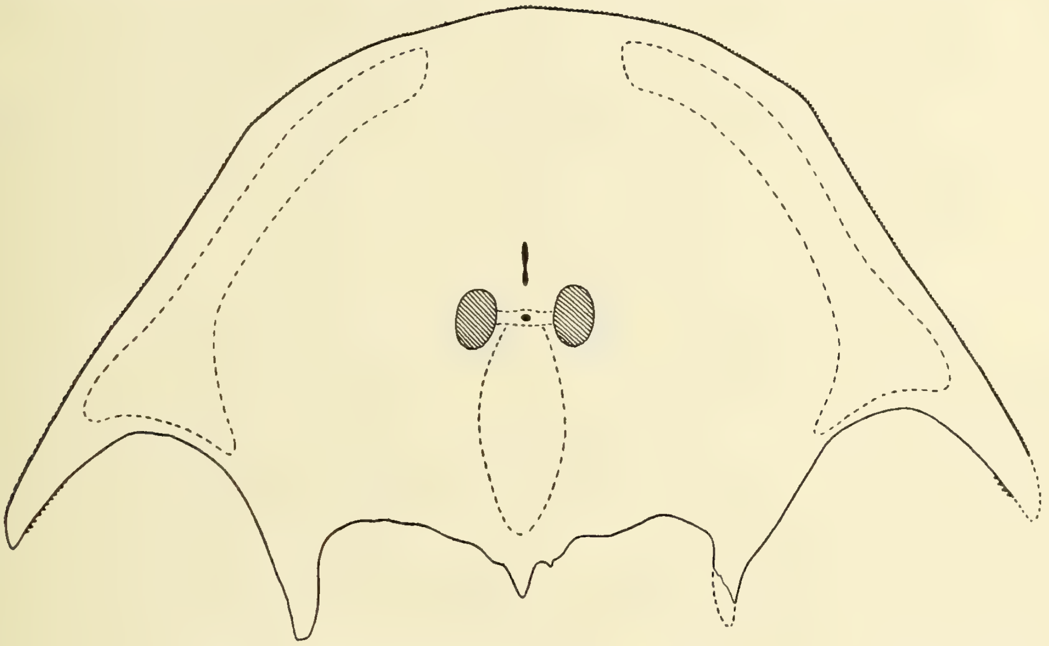
Material.—The available material of this species comprises four cephalic shields, three of which are rather imperfectly preserved. These four cephalic shields belong to the following Museums : the British Museum (the holotype and no. 46569), the Museum of Practical Geology, London (no. 47810), and the Hereford Museum (not numbered).

Description.—The dimensions of the cephalic shield can be measured accurately only in the holotype, in which they are as follows : length from the rostral end of the shield to the posterior end of the inter-zonal part, about 3·35 cm.; breadth across the posterior ends of the cornua (maximum breadth), about 5·8 cm.; height at posterior end of the inter-zonal part (maximum height), about 0·5 cm.; distance from the tip of each cornu to the rostral end of the shield, about 4·3 cm.; distance from each postero-lateral angle to the rostral end of the shield, about 3·7 cm.; and finally, breadth of the inter-zonal part at hinder end, about 2·6 cm. As the holotype has probably been modified by pressure dorso-ventrally, it is likely that in its present state it is somewhat broader and longer than before fossilization.

The other three shields are somewhat smaller than the holotype.

From these measurements it appears that this species attained approximately the same size as *B. holtedahli* and *B. lankesteri,* but it is clear that the maximum breadth of the cephalic shield was less than in either of those species.

The rostral margin of the cephalic shield is obtusely rounded and a rostral angle is present, though, as in *B. lankesteri,* this angle is rather inconspicuous. At the boundary between the rostral margin and each lateral margin there is, as also in *B. lankesteri,* a distinct, obtuse angulation. The lateral margin of each side is more definitely concave than in the other English species. The cornua project diagonally backwards and are rather slender and considerably longer than in *B. lankesteri,* their length constituting about one-fourth of the distance from their tips to the rostral end of the shield. Their inner margins are, at least posteriorly, furnished with small denticles, which are curved forwards in the normal way. The pectoral sinuses are fairly broad, but deeper and better defined than in either of the other two species. The inter-zonal part, however, resembles that in both *B. holtedahli* and *B. lankesteri* in that it reaches backwards beyond the tips of the cornua. Its postero-lateral angles are well developed and extend further backwards than the posterior angle, its posterior margin between the posterior angle and each postero-lateral angle is very concave, and it is destitute of both a dorsal spine and a distinct



TEXT-FIG. 56.—*Benneviaspis anglica,* sp. nov. Cephalic shield in dorsal view. Mainly after the holotype, specimen no. 46568 in the British Museum. Slightly more than × 2 diam.

dorsal median crest: it also decreases markedly in breadth backwards, but not nearly so rapidly as in the other two species. The orbital openings, which may be either somewhat oval or rounded, are in the holotype situated somewhat nearer the rostral end of the shield than the posterior angle. The dorsal electric field is narrower in proportion to its length than in *B. lankesteri*, and its maximum width seems to be situated a little further forwards than in that species. As it is imperfectly preserved, its exact shape is difficult to make out, but it seems to narrow uniformly both backwards and forwards from the middle of its length. The lateral electric fields are not well enough preserved to show clearly the outlines of their middle and anterior parts, but their posterior parts resemble closely in form those of *B. lankesteri*.

The endoskeleton of the cephalic shield is strikingly well ossified: in fact, it seems to be almost as completely ossified as in *Kiaeraspis* and several other Cephalaspids from the Spitsbergen Downtonian. In the holotype it is clear that the two most anterior nerves of the lateral electric field ran in a common canal forwards to a point nearer the orbital opening than the anterior part of the lateral electric field; and, moreover, the same specimen shows that the canal of the dorso-lateral superficial vein 3, at least on the left side, does not open into the orbit but joins the canal of the dorso-lateral superficial vein 4. The canal formed by the union of these two vein-canals opens into the canal of the v. capitis lateralis somewhat behind the orbital opening. Finally, several other canals, both of nerves and vessels, are beautifully displayed in the holotype (Pl. 48, fig. 2).

The exoskeleton of the cephalic shield is so imperfectly preserved that little of its detail can be seen. It is likely, however, that, as in *B. holtedahli* and *B. lankesteri*, it is provided with a continuous superficial layer. The ventral rim, the ventral surfaces of the cornua, and the rostral and lateral margins are ornamented with numerous small, flat tubercles, which are arranged largely in rows concentric with the rostral and lateral borders of the shield. The ornamentation of the dorsal side of the shield is unknown.

The mucous canal system of the cephalic shield is probably enclosed in the exoskeleton, but is not otherwise known.

REMARKS.—As previously pointed out in the description of *B. lankesteri*, the specimens of *Benneviaspis* in the British Museum were referred to one species in my monograph on the Spitsbergen Cephalaspids. The material of *Benneviaspis* from England now available shows clearly, however, that the specimens just described differ in so many characters from those placed in *B. lankesteri* that they must be considered to represent a distinct species, which I have named *B. anglica*.

B. anglica is in all respects more like, and therefore more closely related to, *B. lankesteri* than *B. holtedahli*. From *B. lankesteri* it differs particularly by the much narrower cephalic shield, the longer cornua, the presence of denticles on the inner margins of the cornua, the deeper pectoral sinuses and perhaps also by a somewhat different arrangement of the ornamentation. From *B. holtedahli* it is easily distinguished by, among other characters, the different shape of the cephalic shield, the much more slender cornua, the presence of denticles on the inner margins of the cornua, the much greater depth of the pectoral sinuses, the much narrower dorsal electric field and the greater breadth posteriorly of the lateral electric fields.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: Leverhill and Cradley, Herefordshire.

Benneviaspis sp.

(Text-fig. 12; Pl. 48, fig. 1.)

In addition to the material of *Benneviaspis* described above there is a fragmentary cephalic shield belonging to the Royal Scottish Museum, Edinburgh (no. 1890.6.29*a*). This specimen lacks both cornua and much of the adjacent parts of the shield, so that its exact shape cannot be seen. The parts preserved, however, are as in *B. anglica*, and it is therefore very likely that it belongs to that species. It has been specially recorded here because it shows beautifully the main vascular canals of the sub-aponeurotic (sub-cutaneous) vascular plexus, and, in addition, parts of the canals of the nerves of the lateral electric fields.

GEOLOGICAL FORMATION AND LOCALITY.—Lower Old Red Sandstone: Cradley, Herefordshire.

GENUS SECURIASPIS nov.

DIAGNOSIS.—KIAERASPINAE with cephalic shield moderately broad and usually depressed. Cornua well developed, projecting obliquely from head-shield and extending backwards almost or quite as far as posterior margin of inter-zonal part. Pectoral sinuses broad, but fairly deep and well defined. Inter-zonal part fairly long and narrow, decreasing in breadth rather gradually backwards, with distinct dorsal median crest and slightly produced posterior angle, but without produced postero-lateral angles. Orbital openings situated rather far backwards, nearer posterior angle than rostral end of shield. Dorsal electric field well developed. Lateral electric fields without any distinct postero-medial angles extending medially on to zonal part. Common canal of first and second nerves of lateral electric fields undivided until somewhat antero-ventrally to orbits, and may be almost as far as lateral electric field. Canal of n. trigeminus proper passing down to oralo-branchial chamber entirely behind canal or canals of two most anterior nerves of lateral electric field. Canal of dorso-lateral superficial vein 3 probably passing up to, and opening into, canal of v. capitis lateralis close behind orbit. Middle layer of exoskeleton of cephalic shield with well-developed radiating canals.

GENOTYPE.—*S. kitchini*, sp. nov.

REMARKS.—This genus belongs to the same group of Cephalaspids as *Benneviaspis, Hoelaspis, Boreaspis* and *Kiaeraspis*, and seems to be most akin to *Benneviaspis*. In the general shape of the cephalic shield it resembles, perhaps, more *Thyestes* than *Benneviaspis*, but in *Securiaspis* the canal of the n. trigeminus proper passes down to the oralo-branchial chamber entirely behind the common canal or canals of the two first nerves of the lateral electric fields, and it is therefore obvious that the relationship of this genus to *Thyestes* is less close than to *Benneviaspis*.

At present two species are known, *S. kitchini* and *S. kingi*, both of which are from the Lower Devonian, but it should be noted that *Cephalaspis staxrudi* Stensiö, from the Spitsbergen Downtonian, shows general agreement with *S. kitchini* and *S. kingi* in the shape of the cephalic shield, and on that account it seems very likely that it will eventually prove to be a species of *Securiaspis* (*cf.* Stensiö 1927, p. 272, text-figs. 68, 69; Pl. 34; Pl. 36, fig. 4; Pl. 37, figs. 1, 2).

1. *Securiaspis kitchini*, sp. nov.

(Text-fig. 57; Pl. 49, fig. 1; Pl. 50, fig. 1.)

1891. *Cephalaspis lyelli* (in part), A. S. Woodward, p. 181 (specimen no. P. 4115).

Diagnosis.—A *Securiaspis* with maximum breadth of cephalic shield, measured across posterior ends of cornua, about one and a half times as great as length in median line. Rostral angle not developed and lateral margins convex. Cornua projecting postero-laterally, rather slender and long, their length being contained about three and a half times in distance of their tips from rostral end of cephalic shield. Inner margins of cornua without denticles. Inter-zonal part decreasing rather gradually in breadth backwards. Dorsal electric field about two and a half to three times as long as broad. Ornamentation of ventral parts of cephalic shield consisting of small more or less elongated tubercles arranged concentrically with margins of shield.

Holotype.—Cephalic shield, in the British Museum (no. P. 4115), Pl. 49, fig. 1.

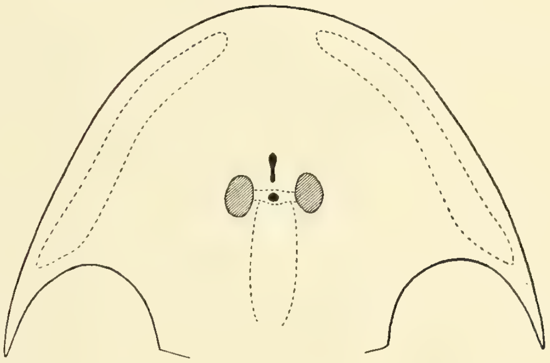
Material.—Two imperfect cephalic shields, one belonging to the British Museum (holotype) and the other to the Sedgwick Museum, Cambridge (A. 3312).

Description.—The dimensions of these two shields are as follows :

	Holotype.	Cambridge specimen.
Length from rostral end to posterior end of inter-zonal part	3 cm.	3·2 cm.
Breadth across posterior ends of cornua (maximum breadth)	4·5 ,,	5·0 ,,
Height at posterior end of inter-zonal part (maximum height)	0·5 ,,	0·6 ,,
Distance from tip of cornu to rostral end of shield .	3·7 ,,	4·0 ,,
Distance from postero-lateral angle to rostral end of shield	3·1 ,,	3·2 ,,
Breadth of inter-zonal part at posterior end . .	2·0 ,,	2·2 ,,

As will be seen from these measurements, the shields are fairly small, and rather flat and broad.

The rostral margin is obtusely rounded, without a rostral angle. The lateral margins are convex. The cornua, which project backwards and somewhat laterally, are slender and fairly long, their length being contained about three and a half times in the distance from their tips to the rostral end of the shield; they are not quite straight but curved slightly inwards, and seem to be without denticles on their inner margins. The pectoral sinuses are fairly broad, but despite this they are deep and well defined. The inter-zonal part, which is rather long, narrows gradually backwards. It reaches approximately as far backwards as the cornua but is imperfectly preserved, so that one cannot tell the form of the posterior angle, or if a dorsal median crest was present. The postero-lateral angles are not produced, and the margin between each of these angles and the posterior angle seems to have been straight or perhaps even somewhat convex. The orbital openings, which are oval or roughly circular in shape, lie behind the middle of the length of the shield measured from the rostral end to the posterior angle of the inter-zonal part. The dorsal electric field is long and narrow, its length being about two and a half or three times as great as the maximum breadth. The lateral electric fields continue for a little way backwards on to the cornua, but they have no postero-medial corners extending medially on to the zonal part of the shield, as in *Benneviaspis*, *Boreaspis*, *Kiaeraspis* and *Thyestes*, and are therefore of the same type as in *Cephalaspis*.



Text-fig. 57.—*Securiaspis kitchini*, gen. et sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. P. 4115 in the British Museum. × 1½ diam.

The endoskeleton of the cephalic shield was well provided with perichondrial bone-layers, and the internal and orbital layers, like most of the canal layers, are strongly developed. In the holotype the common canal of the two most anterior nerves of the lateral electric field on the left side ends fairly close antero-ventrally to the orbital opening, whereas on the right side it continues much further, in fact to a point somewhat nearer the electric field than the orbital opening, before it bifurcates. Moreover, we find in the same specimen that the canal of the n. trigeminus proper of the left side goes down to the oralo-branchial chamber in the space between the two independent canals of the two most anterior nerves of the lateral electric field, whereas the corresponding canal of the right side passes down in the normal way first behind the common canal of these two nerves and then behind the independent canal of the second nerve. Thus in the holotype the arrangement of the n. trigeminus proper and the two first nerves of the lateral electric field were on the left side as in *Cephalaspis*, while on the right side they were developed characteristically for the genus. In the other specimens the arrangement of these organs was typical on both sides. Finally, we find in the holotype that on the left side at least the canal of the dorso-lateral superficial vein 3 does not open into the orbit, but joins the canal of the dorso-lateral superficial vein 4, after which the common canal thus formed goes up to, and opens into, the canal of the v. capitis lateralis somewhat behind the orbit. The specimen belonging to the Sedgwick Museum is too much weathered to display distinctly the vascular canals.

The exoskeleton of the cephalic shield is so imperfectly preserved that one cannot be certain whether the superficial layer was continuous or not. The ornamentation on the ventral rim and of the rostral and lateral margins of the shield consists of small, more or less elongated tubercles, which are arranged concentrically with the margins just mentioned. The ornamentation on the dorsal side of the shield is entirely unknown.

Nothing could be made out concerning the position and development of the mucous canal system.

REMARKS.—The species here described, which is named in honour of Dr. F. L. KITCHIN, of the Geological Survey of Great Britain, is characterized especially by the general shape and proportions of the cephalic shield, the slender cornua projecting only moderately obliquely, the deep pectoral sinuses, and by the rather long dorsal electric field.

GEOLOGICAL FORMATION AND LOCALITIES.—Lower Old Red Sandstone: Kentchurch Hill, Herefordshire; Skirrid Fawr, Monmouthshire.

2. *Securiaspis kingi*, sp. nov.

(Text-fig. 58; Pl. 49, fig. 2.)

DIAGNOSIS.—A *Securiaspis* with maximum breadth of cephalic shield, measured across posterior ends of cornua, almost twice as great as length in median line. [Form of rostral margin unknown.] Lateral margins of cephalic shield rather strongly concave. Cornua projecting very obliquely, slender and long. Posterior half of inner margins of cornua with fairly large, forwardly curved denticles. Inter-zonal part fairly rapidly decreasing in breadth backwards, with median longitudinal crest dorsally. Dorsal electric field about twice as long as broad. Ornamentation of ventral parts of cephalic shield consisting of low, flat tubercles arranged concentrically with margins of shield.

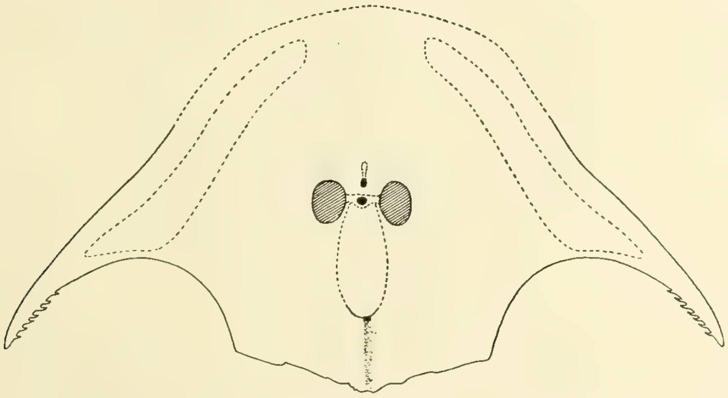
HOLOTYPE.—Cephalic shield, in the Museum of Practical Geology, London (no. 47792), Pl. 49, fig. 2.

MATERIAL.—The species is represented only by the holotype, a fragmentary shield wanting a considerable part of the rostral area and the right cornu.

DESCRIPTION.—This shield is fairly small. On account of its imperfect state of preservation the length from the rostral end to the posterior margin of the inter-zonal part, the distance from the tip of each cornu to the rostral end and that between each postero-lateral angle and the rostral end cannot be measured. The maximum breadth, which falls between the posterior ends of the cornua, may be estimated at about 5·9 cm., and the maximum height, at the posterior end of the inter-zonal part, at about 0·6 cm. The breadth of the hinder end of the inter-zonal part is about 2·1 cm.

Taken as a whole the cephalic shield seems to have been relatively much broader than that of *S. kitchini*.

The rostral margin is unknown. The lateral margins are markedly concave. The cornua, which are more laterally directed than in *S. kitchini*, are slender and fairly long, but nevertheless they do not project backwards beyond the inter-zonal part. Their inner margins bear along the posterior half a few strong, forwardly curved denticles. The pectoral sinuses are broad, but well defined and fairly deep. The inter-zonal part is moderately long and narrows backwards rather rapidly, almost as rapidly as in *Benneviaspis*, and reaches backwards slightly beyond the cornua. Its posterior angle is well developed, and dorsally it is provided with a low, obtuse dorsal median crest. As in *S. kitchini*, the postero-lateral angles are not produced, and the posterior margin between the posterior angle and each postero-lateral angle is only very slightly concave. The orbital openings, which are fairly large and more or less oval in shape, were situated probably nearer the posterior angle than the rostral margin. The dorsal electric field is shorter and broader than in *S. kitchini*, its length being only about twice as great as its maximum breadth. The lateral electric fields, which continue for a short distance backwards on to the cornua, seem, as in *S. kitchini*, to be without the postero-medial angle, which in *Benneviaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis* stretches for some distance medially on to the zonal part just in front of the pectoral sinus. The endoskeleton of the cephalic shield is fairly well ossified. Parts of the internal perichondrial bone-layers, as well as of the orbital bone-layer and canal layers, are distinctly seen.



Text-fig. 58.—*Securiaspis kingi*, gen. et sp. nov. Cephalic shield in dorsal view. After the holotype, specimen no. 47792 in the Museum of Practical Geology, London. × 1½ diam.

Whether the exoskeleton of the cephalic shield is provided with a continuous superficial layer it is impossible to decide. The ornamentation of the ventral rim and the ventral surfaces of the cornua consists of low, flat tubercles, which are somewhat lengthened and arranged concentrically with the rostral and lateral borders of the shield. The ornamentation of the dorsal surface of the shield is unknown. The polygonal areas seem to be fairly large, at least in the posterior parts of the shield.

Remarks.—This species, named in honour of Mr. W. Wickham King, is distinguished by its great breadth, its relatively long and obliquely directed cornua, the presence of strong, forwardly curved denticles on the posterior parts of the inner margins of the cornua, the broad but nevertheless deep and well-defined pectoral sinuses, and by the relatively short and broad dorsal electric field. In the shape of the inter-zonal part it is somewhat suggestive of the species of *Benneviaspis*.

Geological Formation and Locality.—Lower Old Red Sandstone : Leverhill, Herefordshire.

Genus THYESTES Eichwald.

1854. *Thyestes*, E. von Eichwald, p. 108.
1857. *Auchenaspis*, P. M. G. Egerton, p. 286.
1870. *Auchenaspis* (in part), E. R. Lankester, p. 56 (excluding *Eukeraspis*).
1891. *Auchenaspis*, A. S. Woodward, pp. 195–198.
1895. *Thyestes*, K. A. von Zittel, p. 553.

Diagnosis.—Kiaeraspinae with cephalic shield slightly broader than long. Cornua slender but fairly well developed, extending backwards either as far as, or slightly beyond, inter-zonal part. Pectoral sinuses narrow but well defined and usually deep. Inter-zonal part completely closed ventrally, exceedingly long, consisting of about 7 or 8 segments, and decreasing in breadth gradually backwards; postero-lateral angles not produced. Orbital openings situated very much nearer anterior than posterior margin of cephalic shield. Dorsal electric field short, extending backwards only as far as supposed opening of ductus endolymphaticus. Lateral electric fields not extending far forwards nor reaching backwards on to cornua, but with small though distinct postero-medial angles extending medially on to zonal part in front of pectoral sinuses. Common canal of two most anterior nerves of lateral electric field single throughout and lying entirely behind canals of both n. trigeminus proper and n. facialis. Superficial and middle layers of exoskeleton of cephalic shield imperfectly developed. No vestiges present of anterior dorsal fin or crest. Squamation of anterior part of trunk in each transverse row below dorsal series of broad, unpaired and fairly flat ridge-scales, consisting of one high lateral scale, one ventro-lateral scale and probably a number of ventral scales.

Genotype.—*T. verrucosus* Eichwald.

Remarks.—The genus *Thyestes* was imperfectly defined by Eichwald in 1854, but two years later Pander (1856, pp. 44–47) re-described the genotype, *T. verrucosus*, and published new figures of it. Pander did not then, however, consider *Thyestes* to be a distinct genus, but referred the genotype to *Cephalaspis*. Further contributions to our knowledge of the genotype have been published by Eichwald (1860, p. 1532), Schmidt (1866), Rohon (1892, p. 13; 1895; 1896; and 1897), Patten (1903*a*, p. 846, fig. 9), Jaekel (1921, p. 229, text.-fig 9) and by the present writer (Stensiö 1927, Pl. 48, fig. 1).

In 1857 Egerton founded the genus *Auchenaspis*. This genus was further dealt with by Lankester in 1870 (p. 56), who not only added a second, new species to it, but also, though with doubt, described *Eukeraspis* (*Sclerodus*) as a sub-genus of it. A. S. Woodward (1891, p. 195), after having studied the genotype of *Thyestes*, concluded that *Auchenaspis* was identical with *Thyestes* and united both of them under the former name. Woodward's opinion on this matter has been confirmed by later researches, but as the generic name *Thyestes* has priority, it must under current rules of nomenclature be preferred to *Auchenaspis*.

At present three undoubted species of the genus *Thyestes* are known, *viz. Thyestes verrucosus* Eichwald, *Thyestes salteri* (Egerton) and *Thyestes egertoni* (Lankester). The fragment described by Chapman (1906; *cf.* also 1914, p. 259) as *Thyestes magnifica* certainly does not belong to a species of *Thyestes*, and it is very doubtful whether it is from a Cephalaspid at all; neither does "*Cephalaspis schrenckii*" (PANDER 1856, p. 47), which was referred to *Thyestes* by SCHMIDT in 1894, belong to this genus (see STENSIÖ 1927, pl. 48, fig. 2), but probably represents a genus of its own.

The genus *Thyestes* as here defined ranges throughout the Upper Silurian to about the base of the Devonian. It seems to have had a fairly wide geological distribution, as representatives of it are found both in Oesel and in England.

In the monograph on the Spitsbergen Cephalaspids I expressed the opinion that *Thyestes* was closely related to *Benneviaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis* (STENSIÖ 1927, pp. 288, 291, 294). The detailed researches which have now been carried out on *T. egertoni* show, however, that the relationships between *Thyestes* and the genera just enumerated cannot be so close as I then thought, for, as pointed out in the general account of the sub-family KIAERASPINAE above (p. 152), it differs from them and agrees with *Didymaspis* and *Sclerodus* [*Eukeraspis*] both in the relations of the n. trigeminus proper and the n. facialis to the two first nerves of each lateral electric field and in the forward extent of the lateral electric field. In addition, it is likely that it also differed from *Benneviaspis*, *Securiaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis* in the course of some of the anterior dorso-lateral superficial veins.

1. *Thyestes salteri* (Egerton).

(Text-figs. 4, 59; Pl. 50, figs. 3, 4.)

1857. *Auchenaspis salteri*, P. M. G. Egerton, pp. 286–288, pl. ix, figs. 4, 5.
1870. *Auchenaspis salteri*, E. R. Lankester, p. 56, pl. xiii, figs. 7, 8.
1891. *Auchenaspis salteri*, A. S. Woodward, p. 196, text-fig. 28.
1897. *Thyestes salteri*, J. V. Rohon, p. 23.

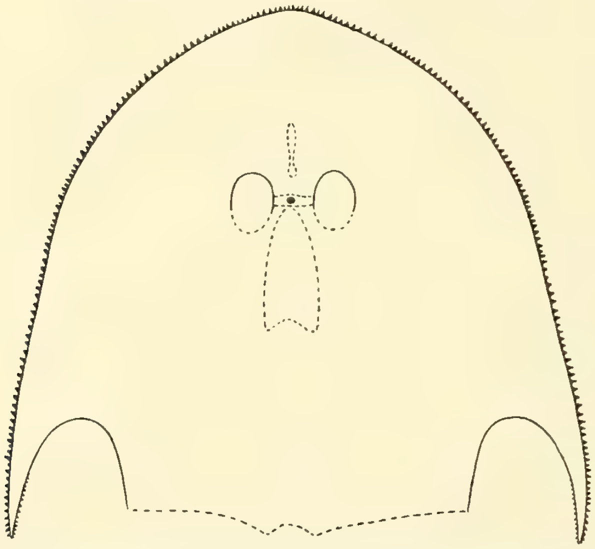
DIAGNOSIS.—A *Thyestes* with maximum breadth of cephalic shield, measured across posterior halves of cornua, only slightly greater than length of cephalic shield in median line. Rostral angle developed. Cornua short and slender, their length being contained between four and five times in distance of their tips from rostral angle; posterior halves of inner margins of cornua with small, straight or backwardly-curved denticles. Pectoral sinuses narrow and deep. Inter-zonal part long and broad. Ornamentation consisting of tubercles which are high and in part rather obtuse on the ventral parts of the cephalic shield.

HOLOTYPE.—Cephalic shield, in the British Museum (no. 45952).

MATERIAL.—Only two cephalic shields belonging to this species have been available to me for study. Of these two shields one belongs to the British Museum (no. P. 674) and the other to the Ludlow Museum (no. D/i/30). The holotype has not been examined by me in detail, and it will not, therefore, be dealt with in the description given below.

DESCRIPTION.—Both the shields studied by me are very small, of approximately the same size. The length from the rostral end to the posterior margin of the inter-zonal part is about 1·2 cm., with a maximum breadth, measured across the posterior ends of the cornua, of about 1·45 cm. The maximum height, which is, as usual, situated in the inter-zonal part, varies from 0·2 cm. to 0·3 cm. The distance from the tip of each cornu to the rostral end of the shield measures from 1·3 cm. to 1·5 cm., and the distance from each postero-lateral angle to the rostral end of the shield about 1·3 cm. Finally, the breadth of the inter-zonal part at the posterior end is slightly more than 0·85 cm. Thus both the shields are very small.

Taken as a whole, the cephalic shield is rather narrow in proportion to its length. Its rostral margin is provided with a distinct rostral angle. The cornua, which project very slightly laterally, are slender and short, their length constituting only about one-fourth of the distance from their tips to the rostral angle. In the shield belonging to the British Museum (no. P. 674) they extend backwards slightly beyond the inter-zonal part, but whether this was also the case in the shield belonging to the Ludlow Museum cannot be made out, as this specimen is considerably distorted. The posterior parts of their inner margins bear a series of very small denticles, which are either straight or bent slightly backwards. Their outer, or lateral, margins are, like the lateral and rostral margins of the shield, armed with a series of high, straight tubercles. The pectoral sinuses are narrow but deep and well defined. The inter-zonal part is broad and long, and decreases gradually in breadth backwards. It is imperfectly preserved in both specimens, but it seems likely that it was complete ventrally and bore a dorsal median crest. The orbital openings are imperfectly preserved, but as far as can be judged they were somewhat oval in shape, and, it should be noted, they are situated much nearer to the rostral angle than to the posterior margin of the inter-zonal part; in fact, they lie at a distance measured from the rostral angle of one-third of the length of the shield. The dorsal electric field is imperfectly preserved in both specimens, but it seems to have been broad posteriorly. The lateral electric fields are also imperfect, but it is obvious that they were well developed.



Text-fig. 59.—*Thyestes salteri* (Egerton). Cephalic shield in dorsal view. Mainly after specimen no. P. 674 in the British Museum. Approx. × 5 diam.

The endoskeleton of the cephalic shield is strikingly well ossified, and its extent within the exoskeletal component is distinctly shown (text-fig. 4). A few branchial fossae (*k*, Pl. 50, fig. 3), the cavities of the two semicircular canals, the canal of the v. capitis lateralis, the canals of the nerves of the dorsal electric field and some of the canals of the nerves of the lateral electric fields are also displayed. The common canal of the two most anterior nerves of each lateral electric field continues undivided down to the field, so that there are no independent canals to be seen at all. This common canal, it should be noted, bends ventro-laterally behind the orbital opening, and throughout its course lies far behind the canal of the n. trigeminus proper.

The exoskeleton of the cephalic shield is so imperfectly preserved that very little detail can be made out. The superficial layer, however, is certainly not continuous. The ornamentation, which could be observed on the ventral rim, on the ventral sides of the cornua, along the rostral and lateral margins and on the sides of the inter-zonal part, consists of tall, rather sparsely and irregularly distributed tubercles. The mucous canal system of the cephalic shield was probably situated entirely superficially to the exoskeleton.

Remarks.—*Thyestes salteri* is well characterized as a species. It is especially distinguished by its small size and its slender and relatively short cornua. Whether it is more closely related to *T. verrucosus* or to *T. egertoni* it is not possible to say as yet with certainty, since our knowledge of the details of the cephalic shield of the former is still very imperfect. It seems, however, rather likely that it is more nearly allied to *T. egertoni*.

Geological Formation and Locality.—Downtonian : Ludlow, Shropshire.

2. *Thyestes egertoni* (Lankester).

(Text-figs. 13, 60; Pl. 27, figs. 3, 4; Pl. 40, fig. 2; Pl. 50, fig. 2; Pl. 51; Pl. 52, figs. 3, 4.)

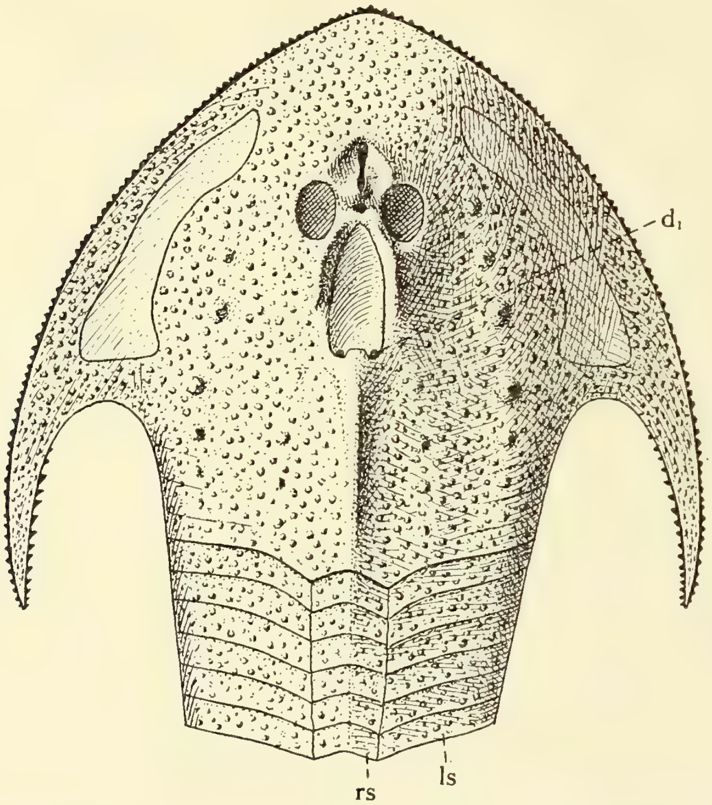
1870. *Auchenaspis egertoni*, E. R. Lankester, p. 57, text-fig. 30, pl. xiii, figs. 3–5.
1891. *Auchenaspis egertoni*, A. S. Woodward, pp. 196–198, text-fig. 29, pl. x, figs. 5, 6.
1897. *Thyestes egertoni*, J. V. Rohon, p. 23.
1898. *Auchenaspis egertoni*, A. S. Woodward, p. 11, text-fig. 11.

Diagnosis.—A *Thyestes* with maximum breadth of cephalic shield, measured across posterior parts of cornua, somewhat exceeding length of cephalic shield in median line. Rostral angle very well developed. Cornua slender and fairly long, their length being contained about three times in distance of their tips from rostral angle; inner margins of cornua with rather large, forwardly curved denticles. Pectoral sinuses narrow and very deep; inter-zonal part long and rather broad. Ornamentation consisting of tubercles, the largest on dorsal side of cephalic shield often arranged in two symmetrical pairs of antero-posteriorly directed lines.

Lectotype.—Cephalic shield, in the University Museum, Oxford (Grindrod Coll., specimen figured by Lankester, 1870, pl. xiii, fig. 3); hereby chosen.

Material.—The available material of this species consists of not less than forty specimens, thirty-eight of which belong to the British Museum [nos. 36187–36190, 46954, P. 675 *a–g* (7 spec.), P. 3237 *a–c* (3 spec.), P. 5314–5316, P. 5083 *a–c* (3 spec.), P. 5371 *a–d* (4 spec.), P. 6023, P. 6112, P. 6113 *a*, *b* (2 spec.), P. 8831 *a–d* (4 spec.), P. 8832–P. 8836], one to the Hereford Museum and one to the Geologisch-Palaeontologisches Institut of the University of Tübingen (no. 1751). Among these forty specimens only four display parts, all more or less fragmentary, of the trunk (Brit. Mus. nos. P. 5316, P. 6023, P. 8832, P. 8836). All the other thirty-six consist of detached, more or less imperfect cephalic shields only.

Description.—The species is of a small size. The combined length of the trunk and cephalic shield cannot have exceeded 5 cm., and was probably less. The cephalic shield, from the rostral end to the posterior end of the inter-zonal part, is between 1·55 and 2·2 cm. long. Its maximum breadth, which falls between the posterior parts of the cornua, is between 2·1 cm. and 2·7 cm., and the maximum height, at the posterior end of the inter-zonal part, varies between 0·3 cm. and 0·5 cm. The distance from the tip of each cornu to the rostral end of the shield is from about 2 cm. in the smallest shields to about 2·9 cm. in the largest. The distance from one of the postero-lateral angles of the inter-zonal part to the rostral end of the shield varies from about 1·6 cm. to about 2·2 cm., according to the size of the shield. Finally, the breadth of the inter-zonal part at the hinder end ranges from 1·1 cm. in the smallest shields to about 1·3 cm. in the largest. It should be noted that several of the shields are flattened dorso-ventrally by pressure, so that they are now broader and lower than before fossilization.



TEXT-FIG. 60.—*Thyestes egertoni* (LANKESTER). Cephalic shield in dorsal view. Mainly after specimen no. P. 6112 in the British Museum. × 4 diam.

d_1, canal probably for a vein from the dorsal electric field and the ductus endolymphaticus; *ls*, lateral scales; *rs*, dorsal ridge-scales.

In general shape the cephalic shield is fairly narrow in proportion to its length, and a very distinct rostral angle is always developed. The cornua, which project in a very slightly oblique direction, are longer than in *T. salteri*, and reach backwards somewhat beyond the inter-zonal part, their length constituting about one-third of the distance from their tips to the rostral angle. Their inner margins are armed with denticles which are directed forwards. Their lateral (outer) margins bear, like the rostral and lateral margins of the shield, relatively high tubercles. The pectoral sinuses are well defined, being very deep but rather narrow. The inter-zonal part is completely closed ventrally; its postero-lateral angle is not produced, nor is its posterior angle developed as such, but is broad with a wide emargination for the reception of the most anterior dorsal ridge-scale of the trunk. On the dorsal side the inter-zonal part is provided with a median dorsal crest, which decreases in height posteriorly so as to be more or less inconspicuous at the hinder end of the shield. In several specimens the inter-zonal part still exhibits traces of the three most posterior transverse rows of scales, by the fusion of which its exoskeleton has been formed, and in exceptional cases faint indications of a fourth are also to be seen. The orbital openings, which are of moderate size, are, as in *T. salteri*, situated very far forwards, at a distance from the rostral angle equal to about one-third of the length of the shield. The dorsal electric field reaches backwards only to the supposed openings of the ductus endolymphaticus, and its length is about twice as great as its maximum breadth, which is situated near the posterior extremity. The lateral electric fields do not extend as far forwards as in most Cephalaspids, nor do they reach backwards on to the cornua; they are pointed in front and broad posteriorly, where each is produced into a small, though distinct, postero-medial angle. Their posterior ends are situated unusually far inwards, in fact immediately in front of the pectoral sinuses.

The endoskeleton of the cephalic shield was lined by well-developed perichondrial bone-layers to about the same extent as in *Kiaeraspis* and *Cephalaspis hoeli* from the Downtonian of Spitsbergen, and as a result a number of the internal structures are not infrequently preserved. These structures, which are well shown in the plates, have already been dealt with in the anatomical account in this work (*cf.* pp. 28–47). It should, however, be noted here that the common canal of the first two nerves of each lateral electric field curves downwards towards the field behind the orbital opening and continues down to it without bifurcation, so that only five, instead of six, of these nerve-canals enter each lateral electric field. Moreover, in this species not only the canal of the n. trigeminus proper but also that of the n. facialis goes down to the oralo-branchial chamber in front of the common canal of the two most anterior nerves of the lateral electric field.

The exoskeleton of the cephalic shield is not well preserved in any specimen. It is evident, however, that its superficial layer was not continuous, and that both it and the middle layer were very imperfectly developed. In some cases the middle layer seems to have been so much reduced in the anterior part of the shield that even the radiating canals lay to a certain extent in the overlying soft tissues, although further to the rear of the shield it seems to be better developed. The ornamentation consists of tubercles of three different sizes: very coarse, coarse, fine. The very coarse tubercles are present only on the dorsal surface of the shield in two pairs of rostro-caudally directed rows, the position and extent of which are well displayed in text-fig. 60, although the medial pair is indistinct in several specimens and may be altogether absent. The coarse tubercles are fairly high but probably not very pointed. They occur over the entire dorsal surface of the shield, on its rostral and lateral margins, and on the ventral rim, where they are always fairly closely but irregularly arranged. Lastly, the fine tubercles are found chiefly on the dorsal and ventral surfaces of the cornua, where they have the same irregular arrangement as the coarse tubercles.

No traces of the mucous canal system of the cephalic shield are to be seen in this species, although the presence of this system is indicated by development of the vascular canal system of the exoskeleton in vascular polygons, as in the Cephalaspids in general. This and the much-reduced state of the superficial parts of the exoskeleton of the cephalic shield show that this canal system lay entirely superficially to the exoskeleton as developed.

The ventral visceral skeleton consists of small polygonal plates closely appressed, but it is so imperfectly preserved (Pl. 51, fig. 4) that little else is known of it.

The remains preserved of the trunk indicate that this decreased in breadth fairly rapidly backwards, and was therefore probably short.

The anterior dorsal fin has disappeared completely, for there is not even an unpaired series of dorsal ridge-scutes like those occurring in *Cephalaspis* and *Hemicyclaspis* to represent it. Nothing is known of the other fins.

The squamation of the trunk is unknown in the caudal region. In the part of the abdominal region not included in the cephalic shield it is developed as follows: most dorsally there is an unpaired series of broad and flat dorsal ridge-scales, which decreases in breadth backwards in proportion as the trunk narrows. The most anterior ridge-scale fits into the emargination of the posterior angle of the cephalic shield. Ventrally to this series we find in each transverse row of scales a high lateral scale, a ventro-lateral scale, and ventral scales, but no dorso-lateral scale, for this is without doubt incorporated in the high lateral scale. The ventro-lateral scales are so imperfectly preserved that it is impossible to discover whether they covered any of the ventral surface of this division of the trunk. The ventral scales have not yet been found. In structure and ornamentation the scales probably resembled the exoskeleton of the cephalic shield.

REMARKS.—*T. egertoni* is well distinguished from both *T. verrucosus* and *T. salteri* by the proportions of the cephalic shield, longer cornua, the shape of the dorsal electric field and by the ornamentation.

GEOLOGICAL FORMATION AND LOCALITY.—Downtonian: Ledbury, Herefordshire.

GENUS DIDYMASPIS Lankester.

1867. *Didymaspis*, E. R. Lankester, p. 152.

DIAGNOSIS.—KIAERASPINAE with cephalic shield much longer than broad. Cornua represented by short, obtuse, laterally directed processes which probably did not project laterally beyond pectoral fins. Pectoral sinuses small and shallow, only appearing as emarginations of lateral borders of cephalic shield. Inter-zonal part very long, exceeding cephalic division proper in length and constituting more than one-half of total length of cephalic shield. Ventral side of inter-zonal part completely closed. Electric fields fairly small: dorsal field extending backwards only to supposed canal of ductus endolymphaticus; lateral fields reaching forwards for very short distance but continuing a fair way backwards and inwards, their postero-medial corners being very long. Common canal of two most anterior nerves of lateral electric fields undivided throughout and lying entirely behind canal of n. trigeminus proper, and probably also that of n. facialis, passing down to oralo-branchial chamber. Middle layer of exoskeleton much reduced in anterior parts of cephalic shield and there destitute of distinct radiating canals.

Genotype.—*D. grindrodi* Lankester.

Remarks.—This genus was founded by Lankester in 1867 (pp. 152–154). In 1870, in his monograph on the British Cephalaspids Lankester gave a new description of the genotype and a "diagram-outline" of its cephalic shield. Further contributions to our knowledge of the genus have been made by Woodward (1891, pp. 199–200) and to a certain extent also by the present writer in 1927 (Stensiö 1927, pp. 301–302, text-fig. 80). Woodward in 1891 and the majority of subsequent writers dealing with the Cephalaspids have placed *Didymaspis* in the family Cephalaspidae (Woodward 1891; Goodrich 1909; Koken 1911; Schlosser 1918 and 1923; Abel 1919, etc.). Zittel (1895, p. 554), Rohon (1897, pp. 15, 29) and Woodward in 1902 (p. 55) have, however, referred it to the family Tremataspidae, established by Woodward in 1891.

Didymaspis is represented by a single species, *D. grindrodi*, which in its distribution seems to be limited to the Downtonian of Western England.

In the general shape of the cephalic shield *Didymaspis* is rather suggestive of *Tremataspis*: on the other hand, it differs considerably from *Tremataspis* and agrees with the Cephalaspidae in the presence of cornua and small pectoral sinuses, the presence of long, undivided lateral electric fields, the course of the nerve-canals leading to the lateral electric fields, and in the development of the radiating canals of the middle layer of the exoskeleton where such canals are present. It is therefore much more closely allied to the genera of the Cephalaspidae than to those of the Tremataspidae, and it must therefore be placed in the former family. In this family it seems in the structure of its exoskeleton and the development of its lateral electric fields and nerve-canals to be most closely related to, and to belong to the same group of genera as, *Thyestes* and *Sclerodus* [*Eukeraspis*].

Didymaspis grindrodi Lankester.

(Text-fig. 61; Pl. 45, fig. 1; Pl. 52, fig. 5; Pls. 54, 55.)

1867. *Didymaspis grindrodi*, E. R. Lankester, pp. 152–154, pl. viii, figs. 4–7.
1870. *Didymaspis grindrodi*, E. R. Lankester, pp. 59–60, pl. xiii, figs. 1, 2.
1891. *Didymaspis grindrodi*, A. S. Woodward, pp. 199–200, pl. ix, figs. 7, 8.
1927. *Didymaspis grindrodi*, E. A. Stensiö, pp. 301–302, text-fig. 80.

Diagnosis.—As for genus (only species).

Holotype.—Cephalic shield, in the University Museum, Oxford (Grindrod Coll.).

Material.—The material of this species studied consists of sixteen specimens altogether, of which eight belong to the British Museum (nos. P. 5043, P. 5313, P. 8844–P. 8846, P. 8847*a*, P. 8847*b*, P. 12659), seven to Mr. Wickham King, Hagley,[1] and one to the Naturhistoriska Riksmuseum, Stockholm (no. P. 10; presented by Mr. Wickham King). All the specimens consist only of more or less imperfectly preserved cephalic shields.

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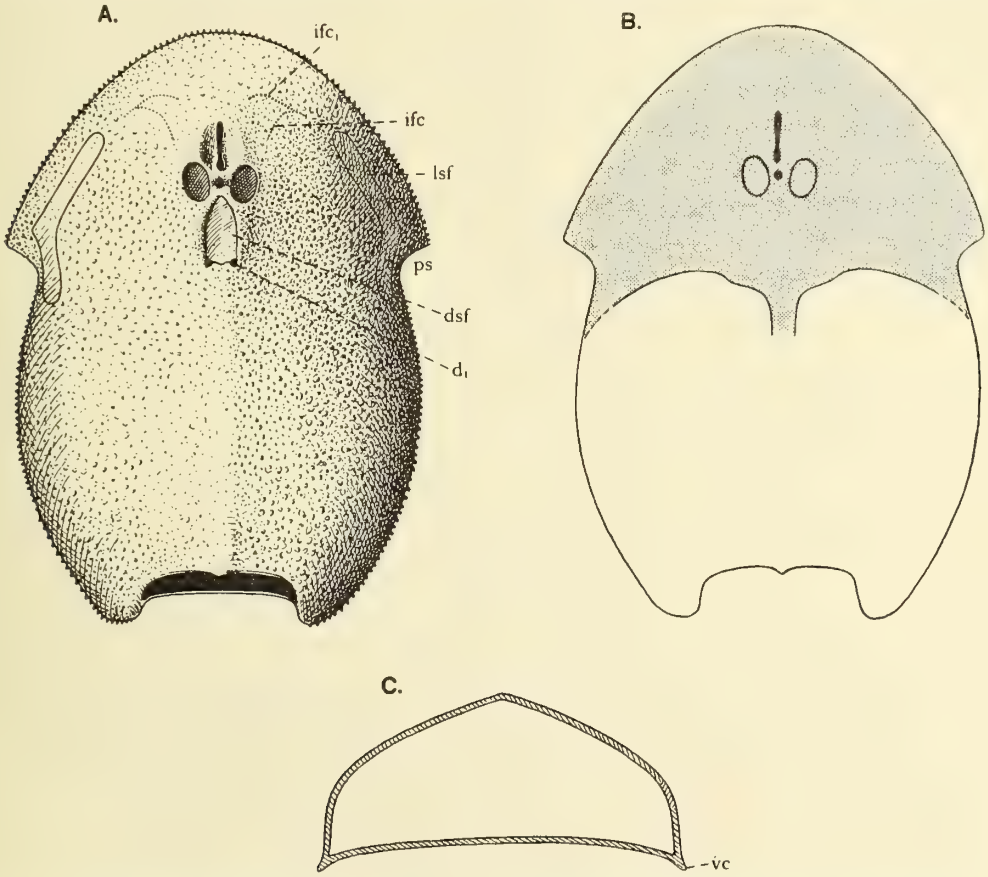
[1] Three of these specimens, figured in Pl. 54, figs. 1–3, and Pl. 55, fig. 1, have since been generously presented to the British Museum by Mr. Wickham King, and are numbered P. 16140–P. 16142.

Description.—The cephalic shields have the following dimensions: the length, measured in median line, varies from 2·5 cm. to 3·4 cm.: the maximum breadth, measured across the posterior ends of the cornua, is in the smallest specimens about 2·1 cm. or 2·2 cm., but in the largest as much as 2·6 cm.: the maximum height, which seems to have been near the junction of the cephalic division proper and the inter-zonal part, and can be measured only in the largest shield, is about 1 cm.: the distance from the tip of each cornu to the rostral end of the shield varies from about 1·4 cm. in the smallest specimens to about 1·8 cm. in the largest; whereas the distance from each postero-lateral angle of the inter-zonal part to the rostral end of the shield varies from about 2·6 cm. to 3·5 cm., according to the size of the specimens: finally, the inter-zonal part is about 2 cm. or 2·5 cm. broad in the middle where it is broadest, but only 1 cm. or 2 cm. at the posterior end where it is narrowest. Thus the species attained only a small size.

It is striking that, owing to the great length of the inter-zonal part, the length of the cephalic shield is so much greater than the maximum width. The rostral margin of the cephalic shield is rounded, without any indication of a rostral angle. The cornua, which project laterally, are so short and indistinct that they form little more than obtuse lateral angles on each side of the shield, and thus it seems likely that they did not project laterally to the pectoral fins, but were as in *Hemicyclaspis murchisoni* (text-fig. 23). If this really was so, we would not, of course, be justified in terming them cornua. The pectoral sinuses are shallow, narrow and without lateral boundaries. The inter-zonal part is very long, as in *Tremataspis,* and as in *Tremataspis, Thyestes* and most other *Osteostraci* it is complete ventrally. In shape it is broadest approximately at the middle of its length, from which point it decreases in breadth both forwards and backwards, especially in the latter direction, so that at its posterior end it is only about one-half as broad as at the middle. Its dorsal surface is convex and bears an obtuse dorsal median crest, whereas its ventral surface is flat or slightly concave. A distinct ventro-lateral ridge is present, as in the scale-covered division of the trunk (text-fig. 61C). The naso-hypophysial aperture is strikingly long, and as usual, it lies at the bottom of a distinct circum-nasal fossa. The orbital openings, which are oval, are situated far forward, in the anterior third of the cephalic shield. The dorsal electric field is short and broad, and does not reach further backwards than to the dorsal opening of the paired canal (d_1), which leads upwards from the occipital vein-sinus to the dorsal surface of the shield and perhaps lodged the ductus endolymphaticus. It is narrow and pointed at its anterior end and broad and slightly concave at its posterior. The lateral electric fields are tolerably well preserved in only one specimen (Pl. 55, fig. 4). On each side of the cephalic shield the field is continuous, as in the other representatives of the CEPHALASPIDAE, and in contrast to those in *Tremataspis,* each of which is divided into two, forming an anterior and a posterior division separated by a considerable space. In *Didymaspis* each lateral field is narrow and reaches only a very short distance forwards, its anterior end being situated some little way behind the infra-orbital sensory canal groove. Moreover, it does not extend backwards on to the cornu of its side, but is provided with a postero-medial process, which is so long that its length constitutes about one-third of the total length of the field and reaches postero-medially across the entire zonal part. The oralo-branchial fenestra is almost circular in outline, being only slightly broader than long. The supra-oral field (*dpr*) is provided with numerous fine, tooth-like tubercles.



TEXT-FIG. 61.—*Didymaspis grindrodi* LANKESTER. A, restoration of cephalic shield in dorsal view. B, outlines of cephalic shield in dorsal view with extent of endoskeleton indicated by shading. C, cross-section through posterior half of inter-zonal part of the cephalic shield. Approx. × 2 diam.

d_1, supposed opening for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf*, dorsal electric field; *ifc*, infra-orbital sensory canal groove; ifc_1, anterior portion of infra-orbital sensory canal groove, which probably corresponds to the anterior part of the supra-orbital sensory canal groove of fishes; *lsf*, lateral electric field; *ps*, pectoral sinus; *vc*, ventro-lateral ridge.

The endoskeleton of the cephalic shield is ossified to about the same extent as in *Thyestes, i.e.* its perichondrial bone-layers are all well developed, and on this account several of the internal structures have been preserved, among others the cranial cavity, the labyrinth cavity, the oralo-branchial chamber and some canals of the nerves of the lateral electric fields. The common canal of the two most anterior nerves of each lateral electric field seems to continue unbifurcated down to the field, and to curve ventro-laterally so far back that both the canal of the n. trigeminus proper and that of the n. facialis lay without a doubt entirely in front of it, although these two canals themselves have not been preserved. It may be noted here that "the line of junction," observed by previous writers between the anterior and posterior halves of the shield, is simply the posterior border of the endoskeleton of the cephalic shield. This border is, of course, to be seen only when the exoskeleton has weathered away or split off.

The exoskeleton of the cephalic shield is especially characterized by the fact that its superficial parts are very imperfectly developed, for, except most posteriorly in the inter-zonal part, not only the superficial, but also the middle, layers are probably entirely absent between the tubercles forming the ornamentation (Pl. 45, fig. 1). Owing to this, we find no radiating canals in most of the anterior part of the cephalic shield; but in the posterior region of the inter-zonal part the basal portion of the middle layer is developed and radiating canals are present. In the micro-structure of the exoskeleton of the cephalic shield *Didymaspis* is a true Cephalaspid, for the radiating canals and the basal layer are quite typical of the family. As has already been mentioned, the exoskeleton of the cephalic shield is ornamented with tubercles, which are fairly closely but irregularly arranged, and rather fine and obtusely conical in shape.

The mucous canal system seems to have been present, but it lay entirely superficially to the exoskeleton, so as to leave no grooves or markings.

The sensory canal grooves are partly displayed in one specimen (Brit. Mus. no. P. 12659, text-fig. 61A, Pl. 55, fig. 3), and it is especially interesting to find that the infra-orbital groove (*ifc*) meets anteriorly a rather well defined groove (ifc_1), which continues postero-medially towards the circum-nasal fossa. This second groove (ifc_1) lies entirely in front of the lateral electric field of its side, and, judging by its position, it may correspond to the supra-orbital sensory canal of fishes: in any case it is clearly the equivalent of the supposed supra-orbital part of the infra-orbital sensory canal-groove of the typical Cephalaspids (see text-figs. 23, 29, 33), although this is, to a large extent, situated on the isolated plates covering the rostral part of the lateral electric field.

Geological Formation and Localities.—Downtonian: Ledbury and Bush Pitch, Herefordshire; Man Brook, Trimpley, Worcestershire (see also p. 204).

Genus SCLERODUS Agassiz.

1839. *Sclerodus*, L. Agassiz, p. 606.
1870. *Eukeraspis* (in part), E. R. Lankester, pp. 56, 58–59 (excluding *Plectrodus*).
1887. *Eukeraspis*, K. A. von Zittel, p. 150.
1891. *Eukeraspis* (in part), A. S. Woodward, pp. 193–195 (excluding *Plectrodus*).

Diagnosis.—Kiaeraspinae with cephalic shield more or less triangular in outline. Marginal areas of shield, laterally and postero-laterally to the oralo-branchial chamber, perforated by four large fenestrae. Cornua very long, about twice as long as cephalic shield measured in median line, and projecting directly to rear. Pectoral sinuses shallow and not well defined medially. Inter-zonal part, if developed at all, narrow and probably very short. Dorsal electric field apparently very small, beginning just behind pineal opening and separated from it by prominent swelling.

Lateral electric fields situated dorso-medially to fenestrae of margin of shield and strikingly short, neither reaching far forwards nor backwards on to cornua, and without distinct postero-medial angles. Common canal of two most anterior nerves of each lateral electric field reaching undivided down to field. Canal of both n. trigeminus proper and n. facialis passing down to oralo-branchial chamber in front of common canal of two most anterior nerves of lateral electric field. Middle layer of exoskeleton well developed but without radiating canals. Mucous canal system probably entirely reduced.

GENOTYPE.—*S. pustuliferus* Agassiz.

REMARKS.—Remains of *Sclerodus* were first described by AGASSIZ in MURCHISON'S "Silurian System," published in 1839 (p. 606). The material then available consisted entirely of small fragments of the cephalic shields, and as most of these fragments were of the lateral margins or the cornua, and therefore provided with long, tooth-like cusps, AGASSIZ seems to have mistaken them for imperfect jaws of fishes. At the same time as he described the remains of *Sclerodus*, he gave also a description of a number of other small fragments of jaw-like, skeletal elements, for which he introduced the generic name *Plectrodus*.

In 1857 a short description of a typical, tooth-bearing specimen of *Plectrodus* was published by EGERTON (1857, p. 288, pl. 10, fig. 4).

According to MURCHISON in "Siluria" (1867, p. 241)[1] SALTER was at that time inclined to consider the remains of *Sclerodus* and *Plectrodus* as jaws of Pteraspids or Cephalaspids. In the explanation to plate XXXV MURCHISON added that, according to Dr. J. HARLEY, these remains were "the posterior spines of the cephalic plate of some Cephalaspidean fish." HARLEY was thus the first to realize the true nature of *Sclerodus*.

LANKESTER had at his disposal in 1870 much more material than the earlier writers. Among other specimens his material included two almost complete cephalic shields of *Sclerodus*, and he was thus able to show unequivocally that *Sclerodus* was a Cephalaspid. He united *Plectrodus* with *Sclerodus* and re-named them *Eukeraspis*; which, it should be noted, he considered so closely allied to *Auchenaspis* (*Thyestes*) as to form but a sub-genus of it.

ZITTEL in 1887 (p. 150) adopted the generic name *Eukeraspis*, but restricted it so as to comprise *Sclerodus* only, *Plectrodus* being retained as a separate genus, which he referred to the SQUALIDAE (p. 64).

WOODWARD in 1891 also accepted the generic name *Eukeraspis* (pp. 193–195) and, like LANKESTER in 1870, he included in the genus both *Sclerodus* and *Plectrodus*.

All later writers dealing with the Cephalaspids have retained the name *Eukeraspis*, and most of them seem to have given it the same connotation as LANKESTER and WOODWARD.

The generic name *Eukeraspis*, however, must be dropped, for *Sclerodus* was sufficiently well described and figured by AGASSIZ to be easily recognizable and has priority by more than thirty years.[2]

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[1] "Siluria," 4th edit. The earlier editions have not been accessible to me. (Salter's comment occurs on p. 268 of the 3rd edit. (1859), but Harley's remark is absent: neither is in the 1st edition (1854).—E.I.W.)

[2] The generic name *Sclerodes* was in 1862 introduced for a Coleopteron, but according to current rules of nomenclature both *Sclerodes* and *Sclerodus* must be retained.

Among the material of British Cephalaspids sent to me for examination there was also the fragment of *Plectrodus* described by Egerton in 1857 (p. 288, pl. 10, fig. 4).[1] This fragment shows at once that *Plectrodus* cannot belong, or even be related, to *Sclerodus*; for not only is it devoid of the ornamentation characteristic of *Sclerodus*, but its general appearance is such that it cannot possibly be from either the cornua or any other marginal part of the cephalic shield of *Sclerodus* (Pl. 53, fig. 6 *infra*). Moreover the teeth on this fragment are very different in shape from the marginal cusps of *Sclerodus*, and much resemble the teeth of Arthrodires or Acanthodians; and, finally, the macroscopic structure of the bone of this fragment seems to be rather like that in the Arthrodires. All that is known about it thus seems to prove definitely that *Plectrodus* is not a Cephalaspid but either an Acanthodian or an Arthrodire, and it cannot therefore be a synonym of *Sclerodus*, but retains its original significance, as given to it by Agassiz.

The skeletal fragment described and figured by Rohon in 1893 (p. 120, pl. 1, figs. 28, 29) as a specimen of *Eukeraspis* seems more likely to belong to *Plectrodus*.

Sclerodus seems to have had a very limited distribution, both stratigraphically and geographically, for so far it has been found only in the Downtonian of the West of England.

In spite of the difference in shape of its cephalic shield *Sclerodus* seems nevertheless to be more closely allied to *Thyestes* and *Didymaspis* than to the other Cephalaspids; for in *Sclerodus* the canal of the two most anterior nerves of the lateral electric field passes down to this field posteriorly to the orbit and the canal of the n. trigeminus proper, just as in *Thyestes* and *Didymaspis;* its lateral electric fields reach, as in *Didymaspis*, much less far forward than in *Cephalaspis*, *Hemicyclaspis*, *Benneviaspis*, *Securiaspis*, *Hoelaspis*, *Boreaspis* and *Kiaeraspis;* and the superficial layer of the exoskeleton is much reduced or even absent.

In the structure of the exoskeleton *Sclerodus* differs considerably from all other genera included in the family Cephalaspidae and also from *Tremataspis*, inasmuch as in the middle layer of the exoskeleton, although well developed, the basal vascular canals, instead of being radially arranged, wind about irregularly, and thus do not form vascular polygons, as in all other typical Cephalaspids. We may note here also that in *Sclerodus* there are no traces whatever of the mucous canal system, either in or on the exoskeleton. This fact, together with the absence of vascular polygons in the middle layer of the exoskeleton, seems to show that the mucous canal system in *Sclerodus* had entirely disappeared, a character which at once distinguishes this genus from all other Cephalaspids and from *Tremataspis*.

These special characters of *Sclerodus* are possibly of secondary origin, and as the genus otherwise show many features in common with *Thyestes* and *Didymaspis*, I have considered it best not to establish any new sub-family for it but to place it in the sub-family Kiaeraspinae.

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[1] This fragment is now in the Ludlow Museum.

Sclerodus pustuliferus Agassiz.

(Text-fig. 62; Pl. 52, figs. 1, 2; Pl. 53, figs. 1–5; Pl. 56, fig. 1.)

1839. *Sclerodus pustuliferus*, L. Agassiz, pp. 606, 704, pl. iv, figs. 27–32, 60–62.
1867.[1] *Plectrodus* (*Sclerodus*) *pustuliferus*, R. I. Murchison, p. 241, pl. xxxv, figs. 9–12.
1870. *Eukeraspis pustulifera*, E. R. Lankester, pp. 58–59, pl. xiii, figs. 9–14.
1891. *Eukeraspis pustulifera*, A. S. Woodward, pp. 193–195, text-fig. 27.

Diagnosis.—As for genus (only species).

Lectotype.—Fragment of cornu, in the Institut de Géologie, University of Neuchâtel (specimen figured by Agassiz, 1839, pl. iv, figs. 60–62); hereby chosen.

Material.—The available material of this species consists of eighteen specimens, of which fourteen belong to the British Museum (nos. 35999, 45949, 45962, 45970*a*, 45973, P. 3247, P. 5844, P. 7360, P. 8927, P. 9752, P. 9756–9758, P. 9897), two to the Ludlow Museum (nos. D/g 106*a*, *b*) and two to Mr. W. King of Hagley. All these specimens consist of small fragments of cephalic shields, with the exception of two, nos. 45949 and P. 9756 in the British Museum, both of which are tolerably complete.

Description.—The two cephalic shields mentioned above, both of which are of approximately the same size, have the following dimensions: the length, measured in the median line from the rostral end to the posterior end of the inter-zonal part, seems to have been about 1·8–2 cm.; the maximum breadth, measured between the outer margins of the middle parts of the cornua, and known from only one specimen (no. P. 9756) is 3·6 cm.; the maximum height, which seems to have been close behind the orbital openings, was probably slightly less than 1 cm.; the distance from the tip of each cornu to the rostral end of the shield cannot be directly measured, but may be estimated at 5 cm., and was thus large in proportion to the size of the shield.

As the other remains found so far belong to shields similar in size to the specimens of which the proportions have just been given, it is obvious that the species attained only a moderate size.

The rostral margin of the cephalic shield is imperfectly preserved, so that it is impossible to determine its form. The lateral part of the shield in the cephalic division proper and in the adjacent anterior part of the cornu of each side is perforated by four wide fenestrae (*for*$_1$–*for*$_4$), and as these have their ventral openings situated laterally and postero-laterally to the oralo-branchial fenestra, it is quite obvious that they have nothing to do with the oralo-branchial chamber. The cornua project posterially and are fairly slender but extraordinarily long. Unfortunately they are not so preserved that their length can be directly measured, but it is clear that they were at least twice as long as the cephalic shield measured in the median line. They are much curved inwards and have a distinct pectoral angle (*p. ang.*), but are devoid of denticles on their inner margins. Their lateral margins, however, are, like the rostral and lateral margins of the shield, provided with strong, straight, pointed cusps. A cross-section through a cornu is shown in Pl. 56, fig. 1, and from this it is seen that it is thicker on the inner side than on the outer and that the inner (vertical) surface is slightly grooved longitudinally. The pectoral sinuses are shallow and seem to be indistinctly limited on the inner side. Of the inter-zonal part very little can be said, but it is likely that it was very short or perhaps scarcely developed. The orbital openings, which are oval in shape, seem to be situated rather far behind the middle of the length of the shield measured in the median line; and immediately behind them is a pronounced, moderately long swelling, behind which lay the dorsal electric field. The latter is so imperfectly preserved that its shape cannot be made out, but it is evident that this field, since it begins so much further backwards than in all other Cephalaspids, must have been short. The lateral electric fields are situated medially to the marginal fenestrae, and are strikingly short, for they end just in front of the level of the orbital openings, and do not extend backwards on to the cornua. They have no postero-medial angles.

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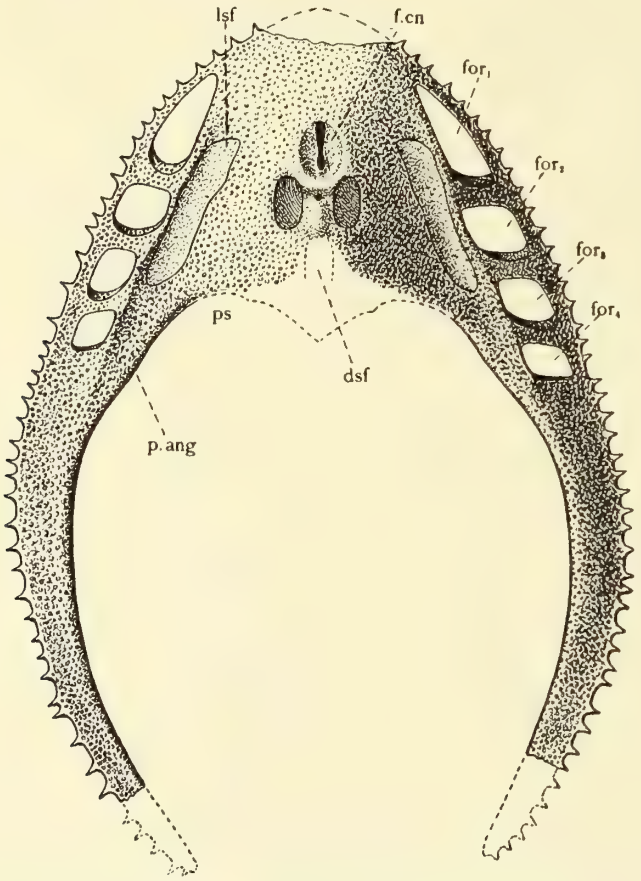
[1] "Siluria," 4th edit. (p. 238, pl. xxxv, figs. 9–12 in the 1st edition.—E.I.W.)



Text-fig. 62.—*Sclerodus pustuliferus* Agassiz. Cephalic shield in dorsal view. After specimens nos. 45949 and P. 9756 in the British Museum. Approx. × 2 diam.

dsf, dorsal electric field; *f.cn*, circum-nasal fossa; for_1–for_4, marginal perforations of the cephalic shield; *lsf*, lateral electric field; *p.ang*, pectoral angle; *ps*, pectoral sinus.

The endoskeleton of the cephalic shield is almost as well ossified as in *Kiaeraspis* and *Cephalaspis hoeli*, and on this account it displays in great detail many of the internal anatomical structures. Among other details, parts of the cranial and labyrinth cavities are to be seen, as well as several of the main vascular sensory canals. The common canal of the two most anterior nerves of each lateral electric field remains undivided as far as its entrance into the field and the total number of nerve-canals entering that field is therefore only five. Both the canal of the n. trigeminus proper and the canal of the n. facialis pass down to the oralo-branchial chamber in front of this common canal.

The exoskeleton of the cephalic shield has no continuous superficial layer, and it is even possible that it was entirely devoid of this layer. The middle layer, on the contrary, is well developed, but in contrast to that in all other Cephalaspids its vascular canals have no radiating arrangement nor are they disposed in vascular polygons. The ornamentation of the dorsal and ventral sides of the shield consists of numerous low, rounded, obtuse tubercles. An ornamentation of similar type is also found on the walls of the marginal fenestrae of the shield, which shows that these perforations cannot have been bridged over or filled with any soft tissue, but were also open when the animal was alive. Along the rostral and lateral margins of the shield there is a series of strong, straight, pointed cusps, which, as already pointed out, continues backwards along the lateral margins of the cornua.

No traces whatever have been discovered of the mucous canal system, either in or on the exoskeleton of the cephalic shield : and since the vascular canals of the middle layer of the exoskeleton of the cephalic shield are not arranged in vascular polygons we may conclude that this canal system had become completely reduced in this form.

Geological Formation and Localities.—Downtonian—from Ludlow Bone upwards: Norton and Ludford Lane, Ludlow, Shropshire; Downton Bridge and Kington (Bradnor Hill), Herefordshire; Baggeridge Colliery, S. Staffordshire.

CEPHALASPIDAE incertae sedis.

"*Steganodictyum*" *carteri* McCoy.

1851. *Steganodictyum carteri*, F. McCoy, p. 483.
1852. *Steganodictium carteri*, F. McCoy, expl. pl. iiA, figs. 4, 4*a*.
1901. *Cephalaspis carteri*, A. S. Woodward, p. 431.

Holotype.—Fragment of cephalic shield; Sedgwick Museum, Cambridge (no. A.3466).

Material.—The only specimens known, the holotype and a small isolated cornu, were not available to me for study.

Description.—Both the original specimen, first described as a sponge, and the cornu are ornamented with fine, elongated tubercles. The cornu is 2·7 cm. long but is imperfect distally; it tapers gradually and has straight sides, of which the outer bears a regular series of broad, backwardly directed tubercles, and the inner, a few larger denticles with apices curved forwards.

Remarks.—These are the only Cephalaspid remains recorded from the marine Devonian of England. It is, however, impossible to define a species based on such fragments, for even the genus is uncertain, although they possibly belong to *Cephalaspis* itself.

Geological Formation and Localities.—Lower Devonian : Looe and Lantivet Bay, Cornwall.

REMARKS ON THE OTHER OSTRACODERMS.

TREMATASPIDAE.

As the organization of the family TREMATASPIDAE was fairly thoroughly dealt with in the monograph of the Spitsbergen Cephalaspids (STENSIÖ 1927, pp. 301–309), it is unnecessary to enter upon it here; but with the extended knowledge which we now possess of the *Osteostraci* in general it is much easier than formerly to denote the main characters by which the TREMATASPIDAE differ from the CEPHALASPIDAE. These characters are: the absence of pectoral sinuses and consequently also of pectoral fins, and the subdivision of the lateral electric fields into well-separated anterior and posterior divisions, with a corresponding grouping of the nerve-canals of these fields. Accordingly the definition of the TREMATASPIDAE which our present knowledge permits is as follows: Cephalic shield well developed and long, extending, with inter-zonal part, far backwards on to trunk. Pectoral sinuses and pectoral fins absent. Each lateral electric field subdivided into two well-separated divisions, anterior and posterior, with nerve-canals correspondingly arranged.

ANASPIDA.

As pointed out by KIAER (1924, pp. 96–97, 100–101) the Anaspids agree in their squamation more closely with the Cephalaspids than with any other forms hitherto known—they have, for instance, like the Cephalaspids, lateral and ventral series of scales well marked off from each other, a similar method of articulation between the scales, the same tendency to form extremely high lateral scales, and an unpaired dorsal series of hollow spines very suggestive of the dorsal scutes which replace the anterior dorsal fin in the CEPHALASPINAE. In addition, the *Anaspida* bear on the axis of the caudal fin nearest the membrane special longitudinal series of small scales which may be paralleled in the other group; and, moreover, they have in the most anterior part of the trunk, between the lateral and ventral series of scales, spines and spinous plates which in several respects are very suggestive of the ventro-lateral scales of the Cephalaspids.

The last-mentioned fact is of very great importance and we shall therefore discuss it in greater detail here.

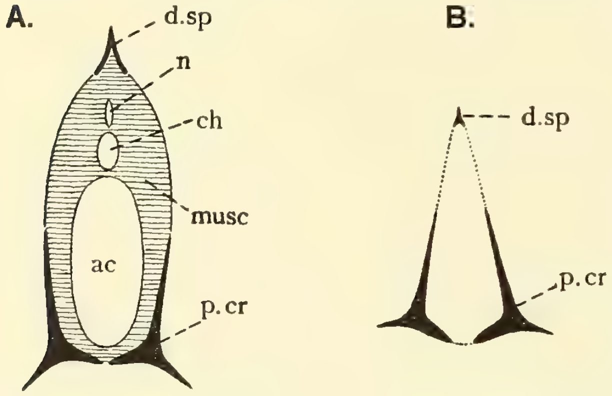
In our study of the British Cephalaspids above we have found that as a rule these have well-developed pectoral fins behind which there is on each side a strong paired ventro-lateral fold (text-fig. 26) reaching backwards for some distance behind the anal opening, and almost to the caudal fin (*cf.* pp. 63–67). This fold, which to judge from its relations probably contains the ventro-lateral part of the trunk musculature of its side, consisted distally of skin only, *i.e.* it was formed by the corium internally and by the epidermis externally. As we have already seen from the description given of the squamation of the Cephalaspids, this fold was provided with a dermal skeleton, which in several forms consists of the ventro-lateral scales alone, but in others, such as *Hemicyclaspis murchisoni*, of the ventro-lateral scales together with the most lateral of the ventral scales. Each ventro-lateral scale viewed on edge (text-fig. 18) is seen to consist of a dorsal (vertical) flange which protects the side of the trunk, a ventro-lateral process supporting the dermal fold, and a ventral flange situated on the under-side of the trunk; the last part is very short or virtually absent in forms such as *Hemicyclaspis murchisoni*. The dorsal flange is overlapped dorsally by the lateral scale of its own transverse row and itself overlaps the ventral end of the lateral scale of the row next behind, thus articulating with the lateral scales of two transverse rows (text-fig. 18).

From the above account it is clear that in *Pterolepis*, *Rhyncholepis*, *Pharyngolepis* (Kiaer 1924, pp. 69–72) and *Birkenia* (Stetson 1928*a*, pp. 467–468) the pectoral plate with its spine (text–fig. 20) is very suggestive of a ventro-lateral scale of the Cephalaspids and that the spines, which in *Pterolepis* (text-fig. 20) follow the pectoral plate and are inserted with their bases between the lateral and ventral series of scales, are very similar to the ventro-lateral processes of the ventro-lateral scales of the Cephalaspids.

We thus find on this point very striking agreement between the Anaspids and Cephalaspids, agreement which seems hard to explain unless we assume that these exoskeletal elements in the two groups have been inherited from common ancestors with strong paired ventro-lateral folds protected by special scales, the distal part of which formed a more or less solid process or spine. Now, as in the Anaspids the pectoral spine-apparatus obviously corresponds to the pectoral fins of the Cephalaspids, whereas the ventro-lateral folds of the Cephalaspids represent the ventral fins, it is, of course, clear that the ventro-lateral folds, which would have been present in the common ancestors of the Anaspids and Cephalaspids, must have reached from immediately behind the branchial region as far back, at least, as the anal opening, and must have corresponded to both pectoral and ventral fins.

The new light which the Cephalaspids throw on the conditions and origin of the paired fins of the Ostracoderms thus seems to prove fully that the paired fins are very old structures which had already been developed in the *Agnatha*, and that the origin of these fins is truly to be found in a paired fin-fold, as predicted by the lateral fin-fold theory. We may note here also that the resemblance of the dorsal spines of the Anaspids to the scutes of the dorsal crest of those Cephalaspids in which the anterior dorsal fin has been reduced suggests that the dorsal spines in the Anaspids may represent a long, transformed dorsal fin, which included the homologues of both the dorsal fins of the Cephalaspids (*cf.* 54, pp. 67–69). In any case it is obvious from the conditions in such Cephalaspids that a fin in the Ostracoderms easily may assume the shape of a strong ridge or crest protected by scale-like or spine-like exoskeletal elements.

Though I consider the pectoral spine-apparatus of *Pterolepis, Rhyncholepis, Pharyngolepis* and *Birkenia* to represent the pectoral part of a paired fin-fold, I do not think it probable that the skin extended between its individual spines, but I imagine that these, though each was covered by the epidermis, were as isolated from each other as in the fossil condition. The pectoral spine-apparatus does not seem, therefore, to have had the function of a balancing or locomotory organ, but seems to have been mainly a weapon of defence, as maintained by Sewertzoff (1928, p. 115). I thus agree with Kiaer with regard to its homologies but with Sewertzoff as to its function.



Text-fig. 63.—*Lasanius* sp. A, a schematized cross-section through the most anterior part of the trunk. The section passes through the body at an angle of about 45° from above downwards and backwards. B, cross-section through the most anterior part of the trunk, according to Bulman (1930). Approx. × 5 diam.

ac, abdominal cavity; *ch*, notochord; *d.sp*, dorsal spine; *musc*, trunk-musculature; *n*, medulla spinalis; *p.cr*, post-cephalic rod.

Having dealt with the pectoral spine-apparatus in *Pterolepis, Rhyncholepis, Pharyngolepis* and *Birkenia* we shall next turn to *Lasanius* in order to deal with the post-cephalic rods, over the homologies and function of which there has been so much controversy (*cf.* Kiaer 1924, pp. 71–72; Stensiö 1927, p. 313; Stromer 1926, 1930; Simpson 1926; Stetson 1927, pp. 249–256; 1928*a*, pp. 459–461; Bulman 1930, pp. 355–357, 358–359; etc.). In my opinion the view advanced by Kiaer, that these rods represent the pectoral spine-apparatus of the other Anaspids, receives strong additional support from the development and relations of the ventro-lateral scales of the Cephalaspids. From the investigations carried out by Stetson (1927, p. 251) it is likely, however, that the rods did not lie at the same level as the scales of the trunk, but a little deeper in the body-wall: despite this there is no reason to consider them as being endoskeletal structures.[1] The fact that the scales of the trunk are thin and ill-developed probably rendered it necessary for the rods to find firmer anchorage in the myosepta basally to the scales (*cf.* Bulman 1930). They had, of course, nothing at all to do with the gills or with the branchial skeleton, which lay entirely in front of them. Moreover, I do not consider it probable that their spines supported a fin-membrane, for these spines seem to be too delicate and to lie

[1] The fact that the post-cephalic rods lack the tubercular ornamentation found on the scales would, according to Stetson (1928*a*, pp. 460–461), be support for his opinion that these rods are endoskeletal structures. This fact, however, has certainly no bearing on this point, for on those grounds we should also have to consider the dorsal spines as of endoskeletal origin, since they also lack tubercular ornamentation (*cf.* Stromer 1926, p. 88).

too far apart from each other for this, but in my opinion it is most likely that their spines projected freely from the body-wall and served mainly as weapons of defence, like the corresponding spines of the other Anaspids.

Of the writers who have dealt with *Lasanius*, BULMAN alone (1930, p. 357) has discussed in detail the shape of its ventral side. He arrived at the conclusion that the ventral surface was more or less flattened. If, however, one takes into consideration that, as normally among vertebrates, the main mass of the trunk-musculature lay dorsally and dorso-laterally to the abdominal cavity, a cross-section through the trunk cannot have been as drawn by BULMAN (see text-fig. 63B), but must have been roughly as shown in text-fig. 63A, although this figure, on account of the oblique direction in which it is supposed to have been taken, is somewhat too high in proportion to its breadth. Under such circumstances the post-cephalic rods cannot have been so disposed that their ascending processes were directed towards the median plane of the animal, but must have been so placed that these processes were either perpendicular or even somewhat inclined outwards from the median plane; consequently, the ventral (ventro-medial) processes must have been either horizontal or so placed that their apices pointed slightly upwards. It follows, therefore, that the ventral surface of at least the most anterior part of the trunk of *Lasanius* must have been either quite flat or even slightly concave transversely, and thus we have here good evidence that in the shape of the ventral surface of the trunk *Lasanius* resembled the Cephalaspids.

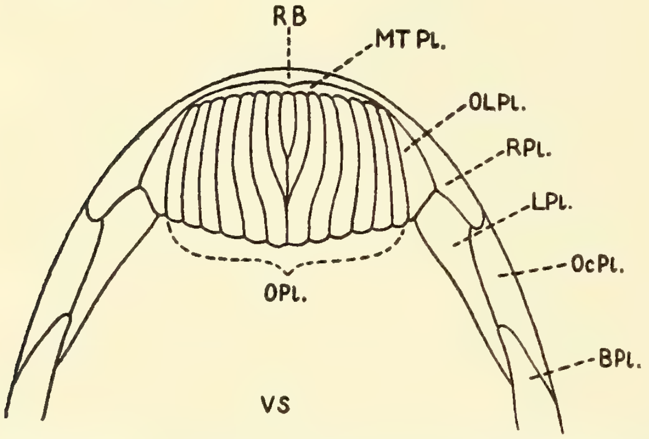
The objections which were raised by SEWERTZOFF in 1928 to KIAER'S opinion as to the systematic position and relationships of the Anaspids have on all main points been refuted by the facts given by the present writer in the monograph of the Spitsbergen Cephalaspids (STENSIÖ 1927, pp. 309–314), and to that account I have nothing of any importance to add here on the subject of the Anaspids.

HETEROSTRACI.

PTERASPIDS.

As I have pointed out elsewhere (STENSIÖ 1927, pp. 315–327) the carapace of the Pteraspids consists in the fossil condition of exoskeleton only, although in the oldest forms it was, as a rule, so closely connected to the endoskeleton that it shows on its internal surface distinct impressions of the latter. In its extent it is clear that it corresponds almost exactly both with the exoskeleton of the cephalic shield and with the main part of the ventral visceral exoskeleton of the Cephalaspids; and, like the exoskeleton of the cephalic shield of the Cephalaspids, it may be provided with a dorsal spine and cornual processes. The material so far known shows that from the Downtonian to the end of Lower Devonian time it underwent a regressive development, gradually breaking up into smaller elements and losing its close connection with the endoskeleton (*cf.* JAEKEL 1911, pp. 30–33; STENSIÖ 1927, pp. 316, 328, 333; KIAER 1928, pp. 121–122).

It was shown by KIAER in 1928 that the mouth-opening, which is situated on the ventral side of the head, is a transverse slit bounded in front by the rostral plate (or its homologue, if the rostral plate is not present as an independent plate) and posteriorly by a series of long, narrow plates, the oral plates (text-fig. 64). These oral plates are, as Kiaer also showed, at least in several forms, provided anteriorly on their upper sides with a thickening, which on its inner sides bears small, tooth-like processes. In addition, Kiaer also found a thickened area bearing similar processes on the inside of the rostral plate, just dorsally to the mouth-opening, and this area, which was termed by Kiaer the maxillary tooth-plate, lies on the antero-dorsal side of the mouth-cavity, immediately above the mouth-opening itself. As the thickenings on the oral plates certainly worked against the maxillary tooth-plate in some way, Kiaer (1928, p. 130) came to the conclusion that the mouth of the Pteraspids " was not a soft, protractile or a suctorial one, . . . but in its function a sort of biting or crushing mouth." He also pointed out that the skeletal elements of the mouth-region are such that they cannot be homologous with the exoskeletal elements of the jaws of the Gnathostomes. Thus the mouth-structure of the Pteraspids has not given rise to that in the Gnathostomes but has developed quite independently of it.



Text-fig. 64.—*Pteraspis vogti* Kiaer. The anterior part of the carapace in ventral view, with the oral plates. After Kiaer 1928. × 3 diam.

BPl, branchial plate; *LPl*, lateral plate; *MTPl*, position of the so-called maxillary tooth-plate; *OPl*, oral plates; *OcPl*, orbital plate; *OLPl*, lateral oral plate; *RB*, rostro-ventral beak; *RPl*, rostral plate; *VS*, ventral shield.

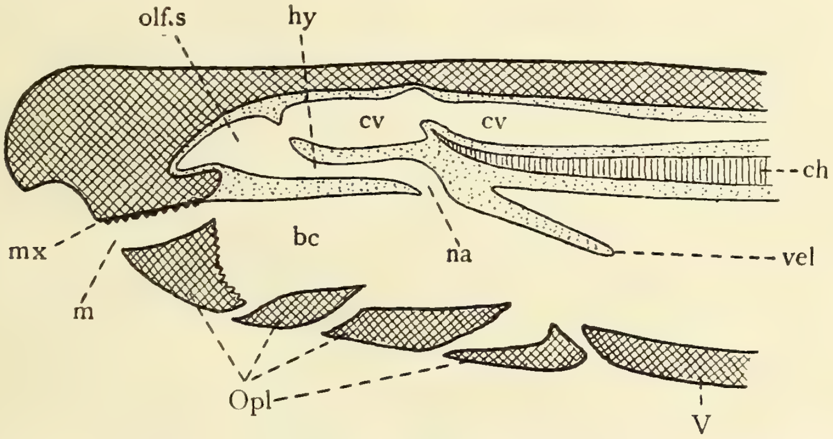
If we consider how the tooth-like tubercles are situated on the so-called maxillary tooth-plate and on the oral plates, we find that these plates cannot have worked directly against each other with their tuberculated surfaces nor could the oral plates have been moved up and down like a lower jaw. In fact, the tooth-like tubercles of the maxillary plate are similarly placed and orientated in the same way as the epidermal tooth on the " ethmoidal plate " of *Myxine*, whereas the tooth-like tubercles of the oral plates, both in position and direction, agree with the epidermal teeth of the rasping organ of *Myxine* when this organ is retracted. In *Petromyzon* the epidermal teeth on the rasping organ are placed more directly forwards, so that the agreement between *Petromyzon* and the Pteraspids in this respect is less than between *Myxine* and the Pteraspids.

From the above remarks it seems very likely that the mouth of the Pteraspids was of the Cyclostome-type, and was already somewhat specialized in a Myxinoid direction : it is, however, beyond question that in all respects it must have been much more primitive than that of the Myxinoids, especially with regard to its endoskeleton and musculature.

A mouth somewhat similarly developed to that in the Pteraspids was proved by

KIAER to occur also in *Drepanaspis, Tremataspis* and the Cephalaspids (*cf.* also pp. 37–38), so that a mouth of Cyclostome-type was thus common to the *Heterostraci* and *Osteostraci*.

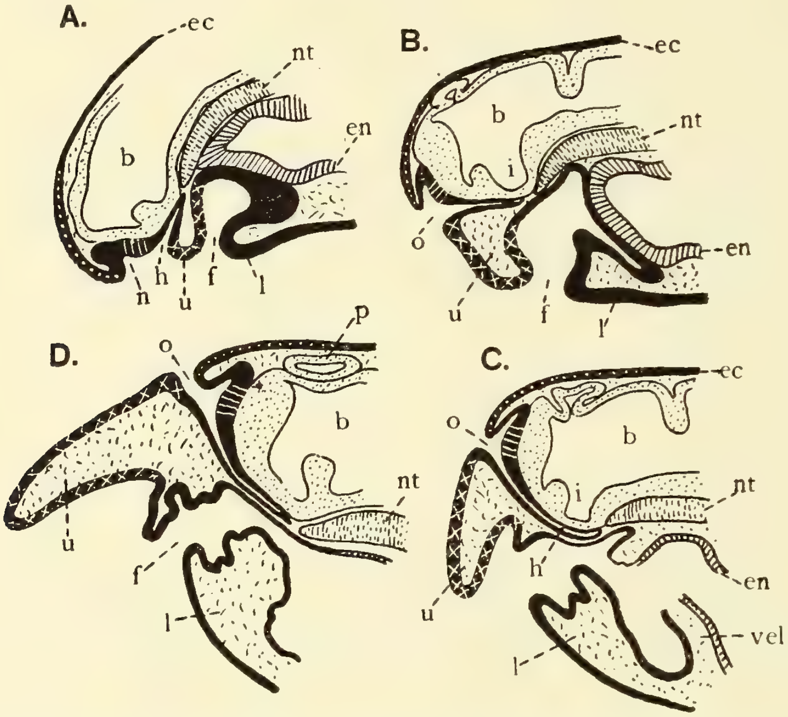
With the much extended knowledge which, since the publication of the excellent paper by KIAER (1928), we now possess of the rostral part of the carapace of the Pteraspids, it is clear that the naso-hypophysial aperture of the Pteraspids cannot have been on the lower side of the rostrum, or on the rostral margin of the dorsal shield immediately in front of the mouth, as I previously maintained (STENSIÖ 1927, p. 323), but in the mouth-cavity itself. Since, to judge from the account given by KIAER, the so-called maxillary tooth-plate stretches along the entire dorsal border of the mouth-opening and extends also somewhat postero-dorsally to it (text-fig. 65), it is obvious that the naso-hypophysial opening must have been situated behind this plate in the roof of the mouth. As the impression of the nasal capsule, which has been found on the internal side of the dorsal shield in several forms, is distinctly paired, it seems possible that the naso-hypophysial aperture was also paired; but for reasons which I shall detail later, I think it more likely that this aperture was unpaired and possibly lay very far backwards, corresponding to the posterior opening of the hypophysial sac of the Recent Myxinoids. My idea of the situation of the olfactory and the hypophysial sacs and their method of opening into the mouth is illustrated in greater detail in text-fig. 65, which is an attempted restoration based on the longitudinal section through the anterior part of the carapace of *Pteraspis vogti* published by KIAER in 1928 (Pl. 12, fig. 2).



TEXT-FIG. 65.—*Pteraspis vogti* KIAER. Diagrammatic sketch of a roughly median longitudinal section through the anterior parts of the carapace, with an attempted restoration of the soft parts surrounding the cavum cerebrale, the olfactory sac and the hypophysial sac. The exoskeleton denoted by cross-hatching, the endoskeleton and other internal structures denoted by dotted lines, and the notochord by vertical lines. Based mainly on the section published by KIAER (1928, Pl. 12, fig. 2). × 10 diam.

bc, cavity of mouth; *ch*, notochord; *cv*, cavum cerebrale; *hy*, hypophysial sac; *m*, mouth-opening; *mx*, maxillary tooth-plate; *na*, naso-hypophysial aperture; *olf.s*, olfactory sac; *Opl*, oral plates; *V*, ventral shield; *vel*, velum.

Analogous conditions to those found in the Pteraspids in regard to the position of the nasal opening are not found in any Recent adult craniate vertebrate. It is true that in the Crossopterygians, Dipnoans and Tetrapods there is an internal nasal aperture in the roof of the mouth, but in all these there is always in addition an external nasal aperture. This being so, it would seem difficult to arrive at a real understanding of the conditions in the Pteraspids with regard to the naso-hypophysial aperture and to compare the Pteraspids in this respect with Recent forms. If, however, we turn to the embryonic development of the anterior parts of the head of the Recent Cyclostomes with special reference to the olfactory organ and the hypophysis, we find that this development throws much light on this point, and on that account it will be necessary to discuss it in detail here.



TEXT-FIG. 66.—*Petromyzon* sp. Four stages in the ontogenetic development of the head. A, youngest; D, oldest stage. Pre-nasal region shown by white dotting, pre-hypophysial region by white lines, and post-hypophysial region by white crossed lines. After Goodrich 1909. Greatly enlarged.

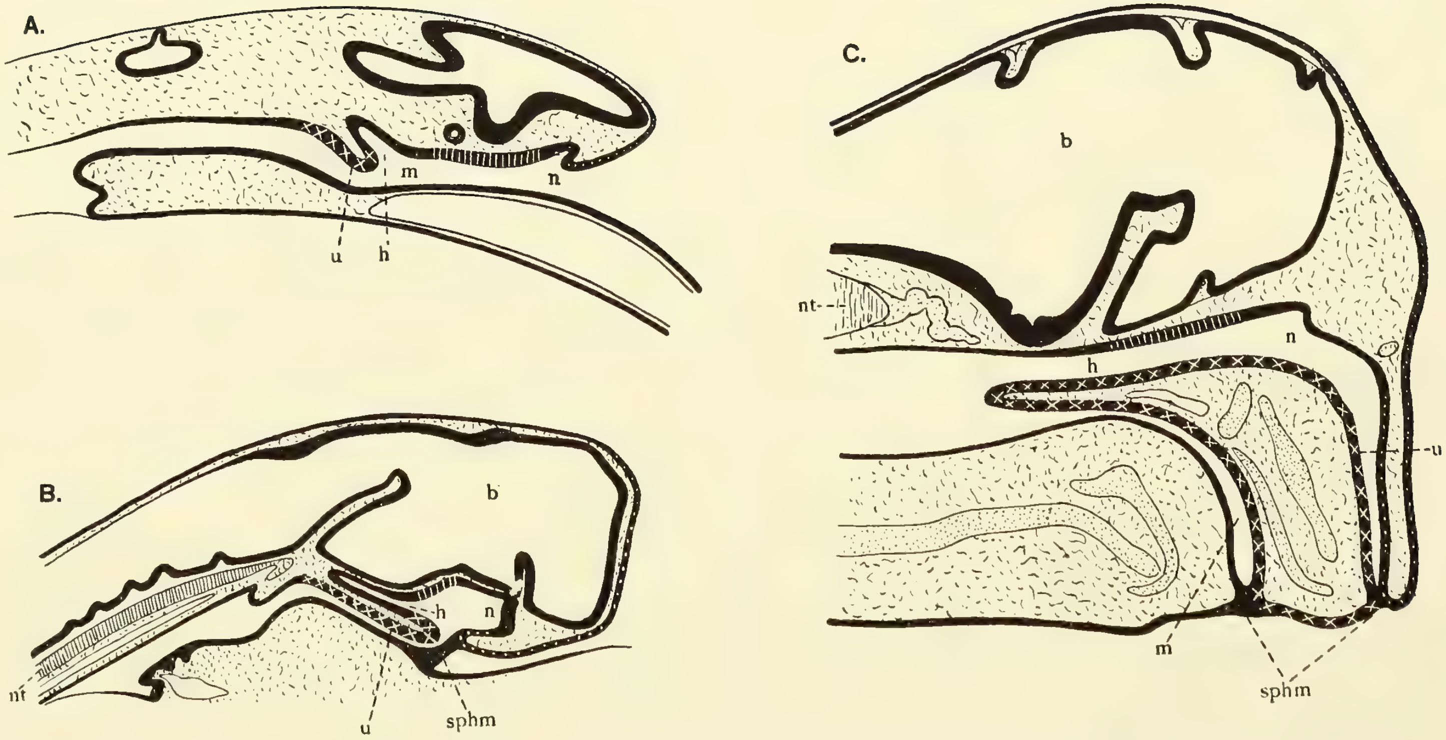
b, brain; *ec*, ectoderm; *en*, entoderm; *f*, stomodaeum; *h*, hypophysial sac; *i*, infundibulum; *l*, lower lip; *n*, olfactory organ; *nt*, notochord; *o*, naso-hypophysial opening; *p*, pineal organ; *u*, post-hypophysial region (upper lip); *vel*, velum.

In the early stages of the Petromyzontids (text-fig. 66A) we find that the olfactory organ and the hypophysial sac are situated on the ventral side of the head, which during this period is much curved downwards anteriorly. Both of these organs open outwards by means of a common, very wide opening. The hypophysial sac is separated posteriorly from the stomodaeum by a fold developed in the post-hypophysial region, a fold which hitherto has usually been called the upper lip, but which we shall term in this account the *post-hypophysial fold*. At a somewhat later stage (text-fig. 66B) the common opening of the olfactory organ and hypophysial sac—the naso-hypophysial opening—has become much more forwardly directed and the post-hypophysial fold has grown considerably larger. At still later stages (text-fig.

66C, D) the naso-hypophysial opening continues to shift, first still more forwards, and then upwards and backwards, until it finally comes to lie on the dorsal side of the head. During this shifting of the naso-hypophysial opening, the post-hypophysial fold increases in size and swings forwards so that finally it forms the rostral part of the head: thus the entire pre-nasal rostral part of the head of the Petromyzontids is formed by the post-hypophysial region of the stomodaeum.

In the Myxinoids the embryonic development is unknown, except in *Bdellostoma*, of which a few stages have been studied (KUPFFER 1899 and 1900; *cf.* also GÖPPERT 1902). In *Bdellostoma* the olfactory organ arises as in the Petromyzontids, *i.e.* on the ventral side of the rostral cranial part of the head (text-fig. 67A). It consists first of an unpaired pit in the median plane, but from this pit a right and a left sac, ending blindly, soon develop, so that to a certain extent it has the appearance of being paired. From this pit a median groove, which includes the primordium of the hypophysis, stretches backwards to a point just in front of the notochord. In somewhat later stages this groove is closed and transformed into a blindly-ending hypophysial sac, which opens anteriorly into the nasal sac (text-fig. 67B). This transformation of the groove into the hypophysial sac takes place in such a way that on each side of the posterior part of the groove there rises a fold which meets and fuses with its fellow of the opposite side in the median line, and grows forwards towards the ventral end of the pre-nasal fold that forms the anterior wall of the olfactory sac. The ventral wall of the hypophysial sac thus formed, which separates the hypophysial sac from the mouth-cavity, was called by KUPFFER the 'archipalate.' This archipalate ends freely somewhat behind the pre-nasal fold, so that at this stage the hypophysial sac and the olfactory organ are in communication with the anterior part of the mouth (text-fig. 67B). Already at this stage there has been formed a secondary pharyngeal membrane (*sekundäre Rachenhaut*) which stretches across from the ventral end of the pre-nasal fold down to the ventral boundary of the mouth-opening, where it fuses with adjacent tissues. In the next known stage, the so-called archipalate has become very thick and strong, especially anteriorly, where it has fused with the secondary pharyngeal membrane (text-fig. 67C): thus at this stage there is neither a mouth-opening nor any external naso-hypophysial opening. An internal naso-hypophysial opening, however, is soon formed at the posterior end of the hypophysial sac, the archipalate being there perforated by a foramen. Finally, at a later stage the secondary pharyngeal membrane disappears both dorsally and ventrally to the anterior end of the archipalate, so that an opening is formed above and below it. Of these openings the dorsal is the permanent external naso-hypophysial aperture, whereas the ventral opening is the permanent mouth-opening. The internal naso-hypophysial opening persists, as is well known, in the adult. The permanent naso-hypophysial opening does not, as in the Petromyzontids, shift upwards and backwards to the dorsal side of the head, but remains in the adult close in front of the mouth, thus having an almost terminal position.

Before leaving the Myxinoids it should be noted that the so-called archipalate, because of its relations to the mouth and hypophysial sac, and despite its somewhat different mode of embryonic development, must certainly be homologous with the



Text-fig. 67.—*Bdellostoma stouti* Lockington. Three stages in the development of anterior part of the head A, the youngest; C, the oldest stage (after Kupffer 1900). Pre-nasal region denoted by white dotting, pre-hypophysial region by white lines, and post-hypophysial region by white crossed lines. All greatly enlarged.

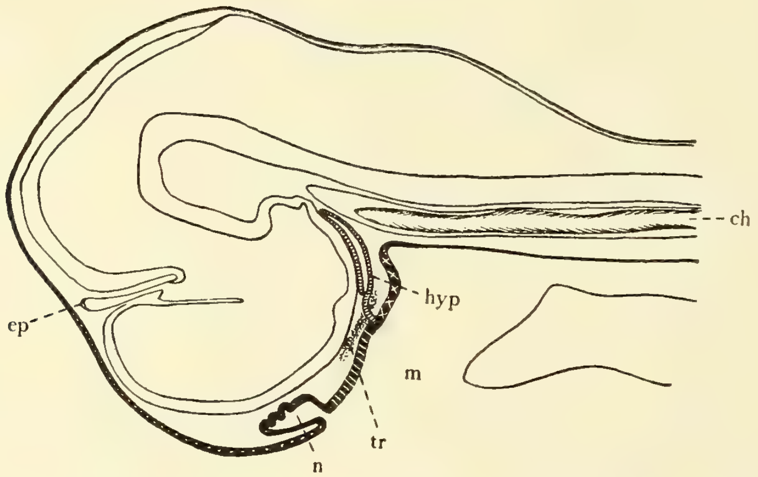
b, brain; *h*, hypophysis and hypophysial sac; *m*, buccal cavity; *n*, olfactory organ; *nt*, notochord; *sphm*, secondary pharyngeal membrane (*sekundäre Rachenhaut*); *u*, post-hypophysial region (upper lip).

post-hypophysial fold (so-called upper lip) of the Petromyzontids, so that this fold is always present in the Cyclostomes, and plays a very important part in the formation of the head. In the Myxinoids it gives rise to the roof of the mouth; in the Petromyzontids, as we have found, it does not form only the roof of the mouth, but in addition it develops there much more strongly than in the Myxinoids and, swinging forwards and upwards, at last forms the whole pre-nasal cranial part of the head. During this process in the Petromyzontids, the naso-hypophysial aperture and the original pre-nasal region of the head are pushed upwards and backwards to the dorsal side of the head, and, as a result, the original pre-nasal region, which finally comes to lie behind the naso-hypophysial aperture, is much suppressed during development.

In fishes and other Gnathostomes (text-fig. 68) the olfactory organ and the hypophysis arise during embryonic development in an essentially similar part of the head as in the Cyclostomes. They remain, however, separated from each other throughout the later stages of development and in the adult. A post-hypophysial fold, stretching forwards and forming the upper boundary of the mouth, does not develop, and the post-hypophysial region thus remains unchanged and has nothing whatever to do with the formation of the mouth-opening. Instead, it is here the pre-hypophysial region which, before the upper jaws have originated, forms the upper boundary of the mouth-opening, and the original pre-nasal region always develops into the rostral part of the head. Accordingly, the embryonic development of the anterior parts of the head of the Gnathostomes takes place in a way fundamentally different from that of the Cyclostomes.

As was shown in 1927 (Stensiö 1927), the Cephalaspids agree with the Petromyzontids both in the development and position of the olfactory organ and hypophysial sac and in the presence of an unpaired external naso-hypophysial aperture, situated on the dorsal side of the head slightly in front of the epiphysis, but far behind the rostral tip of the head. Since these characters are to be found in no other vertebrates except the Anaspids, which are certainly closely allied to the Cephalaspids, and since the Cephalaspids show in other respects such striking agreement with the Petromyzontids that they must be closely related to them, we are led to the conclusion that the pre-nasal part of the cephalic shield of the Cephalaspids is homologous with the pre-nasal cranial part of the head of the Petromyzontids. It follows that the pre-nasal part of the cephalic shield of the Cephalaspids, like its homologue in the Petromyzontids, must have arisen ontogenetically from a post-hypophysial fold, and thus from the post-hypophysial region of the head.

We will now return to the Pteraspids. The skeletal parts surrounding the mouth of these animals agree, as we have seen, in all main features with the correspondingly situated skeletal parts of the Cephalaspids, and on this account there can be no doubt that they are homologous with them. The so-called maxillary tooth-plate is thus certainly homologous with the exoskeletal part of the supra-oral field of the Cephalaspids, and so we are justified in concluding that the upper boundary of the mouth of the Pteraspids has been formed by the post-hypophysial region of the head, exactly as in the Cephalaspids, Anaspids and Recent Cyclostomes. As far as can be judged, a post-hypophysial fold must therefore have been present in the Pteraspids, and of this fold the maxillary tooth-plate must obviously have formed the anterior part only. The part of this fold that lay behind the maxillary tooth-plate must certainly in the normal way have reached backwards to a point somewhat in front of the anterior end of the notochord, and have therefore separated the hypophysial sac and olfactory organ from the mouth-cavity (text-fig. 65). The hypophysial sac was probably widely open to the olfactory sac anteriorly. Since, as we have seen, the Pteraspids completely lack an external naso-hypophysial aperture, and since they cannot have had a completely closed olfactory organ, we must assume that they had instead an internal naso-hypophysial aperture situated somewhere behind the maxillary tooth-plate in the roof of the mouth; but as the post-hypophysial fold certainly extended forwards at least to the anterior border of the mouth, it seems likely that this internal naso-hypophysial aperture was secondary and corresponded to the posterior opening of the hypophysial sac of the Myxinoids. If this be so, it was certainly unpaired and situated far back in the roof of the mouth.



Text-fig. 68.—*Pristiurus melanostomus* (Rafinesque). Median longitudinal section through the head. The nasal pit is projected on to the median plane. After Sewertzoff (1928). Pre-nasal region denoted by white dots, pre-hypophysial region by white lines, and post-hypophysial region by crossed white lines. Greatly enlarged.

ch, notochord; *ep*, epiphysis; *hyp*, hypophysis; *m*, mouth-opening; *n*, olfactory pit; *tr*, trabecula.

The presence of an internal naso-hypophysial aperture in the Pteraspids seems to indicate that in them the anterior part of the head was of the Myxinoid type. This, together with the fact that the anterior part at least of the olfactory sac was evidently situated above the posterior parts of the maxillary tooth-plate (text-fig. 65), renders it likely that the external naso-hypophysial aperture, if developed, would have opened outwards on the ventral side of the rostrum, close in front of the mouth-opening, just as in the Myxinoids; and, if so, its absence is easy to explain by the embryonic development of the Myxinoids, for its absence would beyond question be secondary, due possibly to the persistence of the homologue of the dorsal half of the secondary pharyngeal membrane of the Myxinoids. This, of course, would mean that the post-hypophysial fold of the Pteraspids would have reached forward only to the anterior border of the mouth, and the rostral part of their head would have been formed by the original pre-nasal region of the head.

Thus everything seems to show that the anterior part of the head of the Pteraspids was in the main of the Myxinoid type.

The micro-structure of the exoskeleton of the Pteraspids has been dealt with by several writers, of whom the latest was myself (Stensiö 1927, pp. 317–323). There are, nevertheless, still certain points which have not been thoroughly discussed, above all the question whether it shows any evidence of a mucous canal system corresponding to that of the Cephalaspids, a question to which we shall now turn.

It is well known that in the exoskeleton of the Pteraspids we may distinguish four layers : the basal layer, the cancellous layer, the reticular layer and the superficial layer. Of these, however, it is the reticular and superficial layers only which are of interest to us in the present connection.

The superficial layer (text-fig. 69; Pl. 65, fig. 4) consists of dentine, which, at least in some forms, passes over in its outermost parts into an enamel-like tissue. As we know, it is not present as a uniformly thin, superficial covering of the exoskeleton, but as a rule it occurs in long, flat ridges (*dr*) separated by grooves (*mc*) in which it is entirely absent, thus exposing the reticular layer (*rl*) in the fossil state. In one genus only, *Ctenaspis*, recently described by Kiaer (1930), has it hitherto been found as more or less widely separated tubercles between which the cancellous layer is to be seen, owing to the reduction of the reticular layer. The general occurrence of the superficial layer of the Pteraspids in ridges is very noticeable. These ridges, which for the sake of brevity we shall term here simply the *dentine-ridges*, always lie close to one another, so that the intervening grooves are narrow; but as their lateral surfaces are more or less grooved longitudinally at the base, the grooves between them are considerably wider basally than distally, giving rise to the appearance of being imperfectly closed canals developed for some special system of organs. This appearance, together with the position of their deepest parts in the reticular layer, renders it very likely that these grooves represent the mucous canal system of the Cephalaspids, which, as we have seen, occupies a roughly similar position in the exoskeleton and which also may be partly or entirely represented by grooves. On this account we shall introduce here the term *mucous grooves* for these grooves in the Pteraspids.

In this connection certain features of the Cephalaspids are of especial interest and attention must be drawn to them here. Among the Cephalaspids there are some species with a continuous superficial layer in which the mucous canals, especially on the ventral rim, run parallel with each other or are concentrically arranged. The pores of these canals run straight outwards from their respective canals, so that they lie in distinct rows above them. In each such row they are usually more or less confluent with one another superficially, or, expressed in another way, the superficial layer between the pores is imperfectly developed, so that these rows of pores open into more or less distinct grooves superficially to the mucous canals. As a result of this arrangement, the superficial layer between the parallel or concentric mucous canals becomes more or less completely subdivided into dentine-ridges (Stensiö

1927, pp. 37, 265–266, 273, 320; Pl. 67, fig. 2; Pl. 68, figs. 1–3), which agree essentially with those of the Pteraspids. It is of great importance to find that it is beyond question the mucous canals which give rise to the formation of dentine-ridges and thus to a development of the outer parts of the exoskeleton similar to that in the Pteraspids.

The reticular layer of the exoskeleton of the Pteraspids is characterized by the presence of numerous vascular canals, which seem to correspond to the external branches of the radiating vascular canals of the Cephalaspids and, like those branches, form a sub-epidermal vascular plexus (Stensiö 1927, p. 319). From this plexus branches are seen to pass outwards (*ebc*, text-fig. 69; Pl. 65, fig. 4), both to the pulp-like cavities in the dentine-ridges and to the mucous grooves. As these branches on their entrance into the mucous grooves are relatively wide, the vessels they lodged must, of course, have continued a certain distance in the basal parts of the mucous grooves, a fact which shows beyond question that the bottom of these grooves was not directly lined by the epidermis, but that there must have been a layer of richly vascular connective-tissue. The reason why this connective-tissue was so rich in vessels is difficult to understand unless we assume that the mucous grooves had been developed for a special system of organs for which a plentiful blood-supply was needed. Now since the mucous canal system of the Cephalaspids received its blood from branches of the sub-epidermal vascular plexus, or through external branches more or less directly from the vessels of the radiating canals (and thus quite as the supposed system of organs in the mucous grooves of the Pteraspids), we have here very strong support for the opinion advanced above that this system of organs was the mucous canal system.

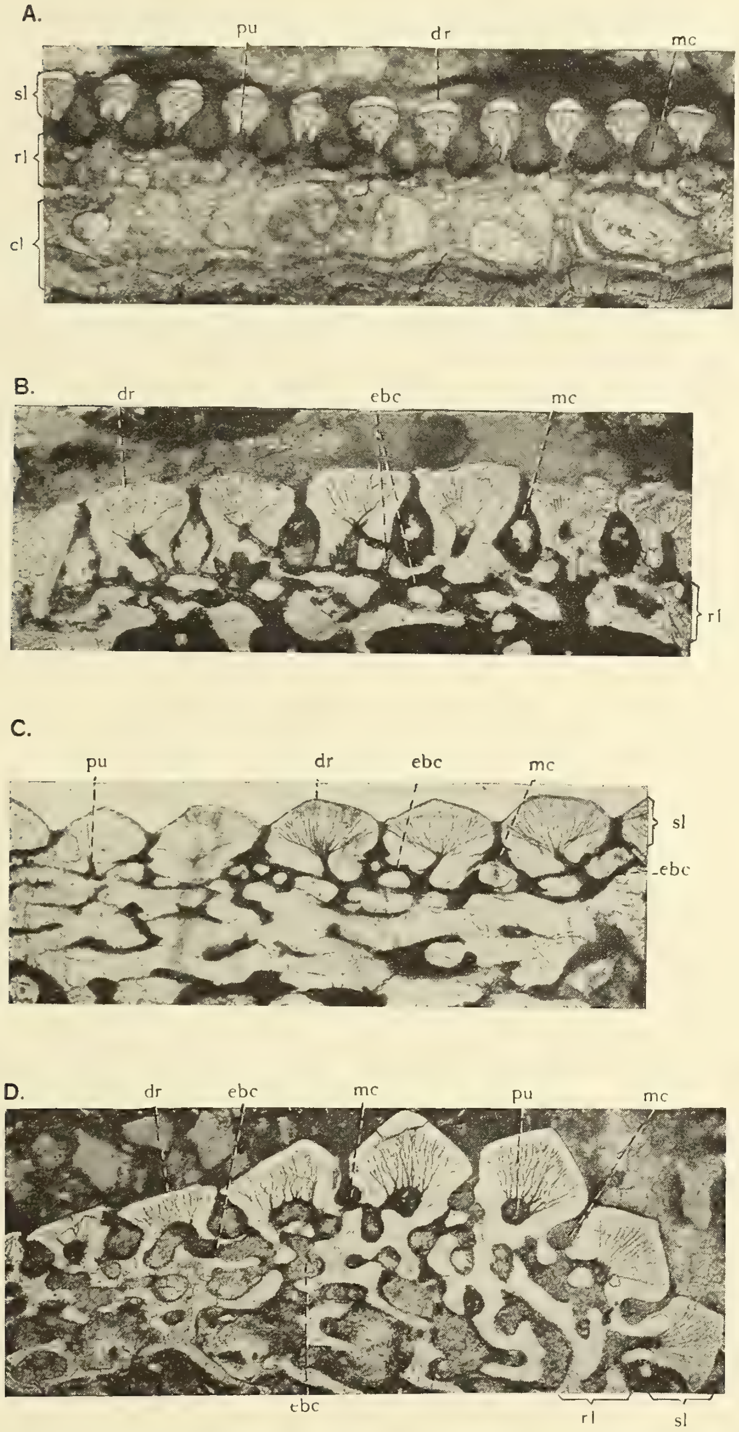
Thus the micro-structure of their exoskeleton seems to show that the Pteraspids had a mucous canal system, and that it was the arrangement of this canal system which caused the remarkably constant development of the superficial layer of the exoskeleton to form dentine-ridges. This development is thus probably a secondary character of the exoskeleton and has nothing whatever to do with its origin.

The presence of the mucous canal system in both the Pteraspids and the *Osteostraci* shows that this system must be very old and have been already developed in the common ancestors of the *Heterostraci* and *Osteostraci*. On this account it is only to be expected that it was developed also in *Heterostraci* other than the Pteraspids: in any case, as we shall see, we find possible traces of it in the Drepanaspidae.

In the Ostracoderms the disposition of the sensory canal system, which is now known in a fair number of forms (*cf.* Stensiö 1926; Kiaer 1928, 1930), is very clearly of a type similar to that in the Petromyzontids, although subject to variations.

The endoskeleton inside the carapace of the Pteraspids must, as I have pointed out in the monograph of the Spitsbergen Cephalaspids (Stensiö 1927, pp. 322–327), have been largely of a similar type to that in the Cephalaspids, whereas the branchial openings were of the Myxinoid type.

The ear of the Pteraspids, as is well shown from impressions of the dorsal side of the otic capsule found on the basal surface of the carapace of the oldest forms, must have been at least in a similar stage of development as, and in any case not



Text-fig. 69.—Sections through the superficial parts of the exoskeleton of Pteraspids. The sections are transverse to the direction of the dentine-ridges. A, from a Pteraspid from the Downtonian of Spitsbergen. Approx. × 100 diam. B–D, from Pteraspids from the Devonian of Spitsbergen. Approx. × 70 diam.

cl, cancellous layer; *dr*, dentine-ridges; *ebc*, vascular canals of the reticular layer; *mc*, mucous grooves; *pu*, pulp-cavities of the dentine-ridges; *rl*, reticular layer; *sl*, superficial layer.

more lowly organized than, in the Cephalaspids. The brain was certainly also in a similar stage of development.

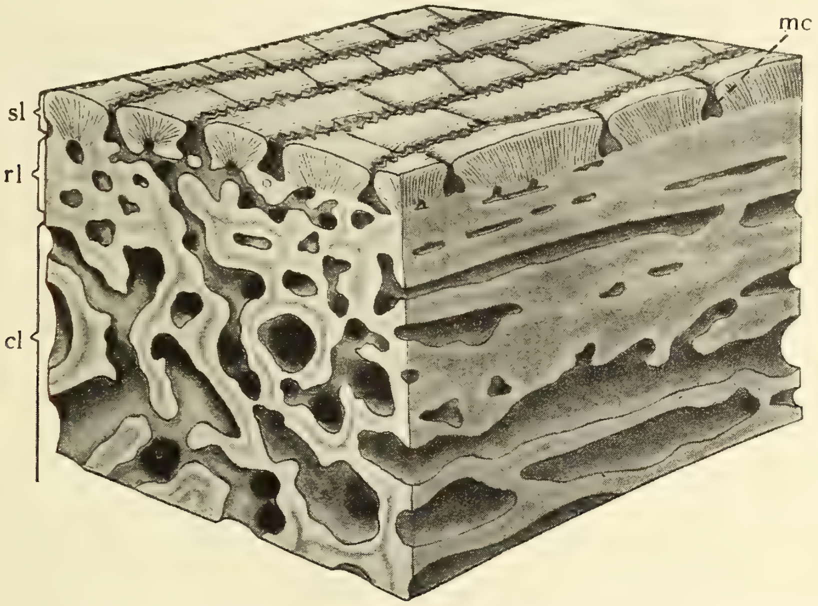
From our present knowledge it is quite evident that the Pteraspids are true Ostracoderms, and have nothing whatever to do with the Elasmobranchs. In the development of the skeletal parts surrounding the mouth, the backward extent of the carapace, the development of the posterior parts of the carapace, the coherence of the endocranium, visceral endoskeleton and endoskeletal shoulder-girdle, the probable presence of a mucous canal system, the disposition of the sensory canal system and the presence of a sub-epidermal vascular plexus in the exoskeleton, they are suggestive of the *Osteostraci.* On the other hand, in the development of the rostral part of the head, the development of the olfactory organ and hypophysis, the mode of opening of the olfactory organ and the hypophysis into the mouth and the development of the external branchial opening, they agree with the Myxinoids. They are thus on the one hand more closely related to the *Osteostraci*, *Anaspida* and Petromyzontids than are the Myxinoids, but on the other they nevertheless appear to belong to the same branch of the Ostracoderms as the Myxinoids. The opinion advanced by the present writer in 1927 that the Ostracoderms diverged into two main branches, one comprising the *Osteostraci*, *Anaspida* and *Petromyzontia*, the other the *Heterostraci*, *Palaeospondyloidea* and *Myxinoidea*, must therefore be maintained despite the objections that have been made to it (Stetson 1928*b*, pp. 226–230; Goodrich 1931, pp. 45–49; De Beer 1931, p. 50).

DREPANASPIDS.

As in the monograph of the Spitsbergen Cephalaspids I had the occasion of discussing the structure of the Drepanaspids (Stensiö 1927, pp. 327–330), I shall confine myself here to giving a few short remarks only.

Since their mouth is developed in a way similar to that in the Pteraspids and they lack an external naso-hypophysial aperture, it is evident that the rostral parts of the head of the Drepanaspids must have been exactly as in the Pteraspids, and that an internal naso-hypophysial aperture situated in the roof of the mouth must have been present.

The exoskeleton of the Drepanaspids generally resembles that of the Pteraspids, but the basal layer is much thinner, and the cancellous layer less distinctly developed, inasmuch as it has smaller sinuses and passes superficially into the reticular layer without any distinct boundary. The superficial layer consists of dentine and perhaps also of enamel in its outermost part; it does not form a continuous covering to the reticular layer, but is present only as tubercles which are separated by more or less wide interspaces. These tubercles agree in their microscopic structure completely with the dentine-ridges of the Pteraspids, and where they are situated fairly close together, the spaces between them are often wider basally than distally and are also otherwise developed in a manner suggestive of the mucous grooves of the Pteraspids. As, in addition, the vascular canals of the reticular layer ascend to these interspaces, it seems likely that these were, indeed, mucous grooves. The development of these supposed mucous grooves is shown in detail in text-fig. 70 and Pl. 66, figs. 5, 6 (*mc*). Since they are present around all the tubercles, the mucous canal system must have formed a network and have been more of the type found in the Cephalaspids than of that in the Pteraspids.



TEXT-FIG. 70.—*Psammosteus maeandrinus* AGASSIZ. Sketch showing the structure of the exoskeleton. Greatly enlarged. From KIAER 1915.
cl, cancellous layer; *mc*, supposed mucous grooves; *rl*, reticular layer; *sl*, superficial layer.

COELOLEPIDS.

In most of their known characters the Coelolepids are very suggestive of the Ostracoderms, especially of the Pteraspids and Drepanaspids (*cf.* STENSIÖ 1927, pp. 330–334), and so they have hitherto been incorporated in the *Heterostraci*. As is well known, however, they differ from the *Heterostraci*, as well as from all the other Ostracoderms, in the development of their exoskeleton, inasmuch as this consists, both on the head and trunk, only of small scales which resemble both the dentine-tubercles and the dentine-ridges of the Pteraspids and Drepanaspids on the one hand, and the placoid-scales of the Elasmobranchs on the other. This development of their exoskeleton has led TRAQUAIR (1899*b*, pp. 853–854) and several other writers, among them STETSON (1928*b*, pp. 226–230; 1931, p. 154), to the conclusion that they were in some way related to the Elasmobranchs. STETSON goes even so far as to maintain that on account of this development of the exoskeleton they are to be removed from the Ostracoderms and to be placed with the Elasmobranchs.

It is true that our knowledge of the Coelolepids is still very imperfect, but what is known of them points very definitely to a close relationship with the *Heterostraci* among the Ostracoderms; and since the Ostracoderms, as we know now, are lowly organized, primitively agnathous vertebrates, it is obvious that there is no reason for considering the Coelolepids to have any Elasmobranch affinities. Scales of the placoid-type have simply arisen independently in the Coelolepids and Elasmobranchs. In this connection it may also be pointed out that the ventral visceral exoskeleton of certain Cephalaspids may also be developed as Coelolepid-like scales (Kiaer 1928, p. 124), from which it is seen that the exoskeleton of the Ostracoderms under certain conditions may easily be reduced and transformed into scales of that kind. We have therefore in this fact a further support for my suggestion (Stensiö 1927, pp. 332–334) that the placoid-like scales forming the exoskeleton of the Coelolepids are not primitive, but have arisen secondarily as a result of regressive development.

For further remarks on the organization of the Coelolepids the reader is referred to my monograph on the Spitsbergen Cephalaspids (Stensiö 1927, pp. 330–334).

⁂

From the above remarks on their organization it is now more obvious than before that the *Heterostraci* are true Ostracoderms which are closely akin to the *Osteostraci, Anaspida* and *Petromyzontia,* but which nevertheless are so typically Myxinoid in the development of the rostral part of the head, the development of the naso-hypophysial aperture and the mode of opening of the gill-pouches outwards that they must be considered to belong to the same main branch of the Ostracoderm stem as the *Myxinoidea.*

PETROMYZONTIA.

The researches of Holmgren on the muco-cartilage of the *Petromyzon*-larva on which I based my comparisons of the endoskeleton of the head of the Petromyzontids and Cephalaspids (Stensiö 1927, pp. 336–350), were carried out on Bouin and Zenker material stained by all recognized methods, and it is of importance here to emphasize that these researches showed clearly that the muco-cartilage of the *Petromyzon*-larva has a larger extent than was maintained by either Schaffer or Gaskell.

In a paper recently published Tretjakoff (1929) has dealt with the muco-cartilage of the *Petromyzon*-larva. He arrived at conclusions concerning the extent of this cartilage that are contrary to those of Holmgren: in fact, Tretjakoff in this paper maintains that the extent of this cartilage in the *Petromyzon*-larva was very limited. As he does not give any information as to the methods employed by him for the study of the muco-cartilage, it is impossible to ascertain why he has arrived at a result so widely different from that obtained by Gaskell, Schaffer and Holmgren.

In order to settle this question definitely Holmgren has recently again taken up his researches, and until his new work has been completed I shall not attempt to discuss Tretjakoff's conclusions on this matter, but shall postpone it until a later occasion.

Tretjakoff in the paper referred to above also objects to the opinion of previous writers that the muco-cartilage is a form of true cartilage, and goes so far as to separate it from the true cartilage, terming it *basophile Gallertgewebe.* In my opinion he has merely created a new term for this tissue without explaining its true nature. The important fact that it has a similar staining power to cartilage seems to be of little significance to him; but whether TRETJAKOFF is right or wrong in this particular case is irrelevant to the point at issue, for it is not as a special form of cartilage that the muco-cartilage has been compared to the endoskeleton in the head of the Cephalaspids, but as a mass of tissue which in its extent, position and relations generally shows many striking points of agreement with it.

Following his opinion on the muco-cartilage of the *Petromyzon*-larva TRETJAKOFF concluded that the Cephalaspids were probably much specialized in the great extent and coherence of the endoskeleton of the head; but since the endoskeleton of the head of all the Ostracoderms must, as we know, have been of a somewhat similar type to that of the Cephalaspids, this type must be very ancient, and its general occurrence in all groups of the Ostracoderms shows that it must have been inherited from the common ancestors of all the known Ostracoderm groups. Thus it is obvious that if the Cephalaspids were highly specialized in regard to the endoskeleton of the head, then so must have been all the other Ostracoderms and their primitive common ancestors as well. This can hardly have been the case, and we are instead forced to assume that the type of endoskeleton found in the head of the Cephalaspids is, on the whole, primitive. It is important to note here that in the Cephalaspids at least the post-branchial wall is so placed beneath the otic capsule and so much inclined forwards that the space above it, even immediately behind the otic capsule, is relatively high and wide, so that there is good reason to assume that the somatic muscles of the fourth and fifth segments persisted, just as in the recent Cyclostomes, although they did not extend so far forwards but retained a more normal position.

That the endoskeleton of the head of the Cephalaspids was of " dermal " origin and not a true endoskeleton, and that other cartilaginous skeletal elements were present internally to it, as TRETJAKOFF seems to believe, are certainly on the whole incorrect; for, as we know, it enclosed the brain, the auditory organs, the olfactory organs, the notochord and in addition most of the nerves and vessels of the head. The only place in which an endoskeleton of hyaline cartilage could possibly have been present internally to the known endoskeleton is in the medial parts of the soft interbranchial septa, but so far, there is no evidence that this was the case. If such skeletal elements had been present, they would, of course, have been situated medially to the branchial nerves and vessels, like the branchial arches of fishes; whereas the branchial skeleton of the recent Cyclostomes, as is well known, lies mainly externally to them, like the visceral endoskeleton of the Ostracoderms. From its extent, position and relations it is thus beyond question that the endoskeleton of the head of the Cephalaspids resembles on the whole that of the recent Cyclostomes, and that, contrary to the opinion of TRETJAKOFF, it also includes the homologues of its hyaline cartilages.

TRETJAKOFF'S objections to the interpretation of the pectoral fin-flap of the Cephalaspids as a pectoral fin is in the present work shown to be untenable (*cf.* pp. 63–64).

Finally, we may note here that TRETJAKOFF was in doubt whether the superficial layer of the exoskeleton of the Cephalaspids really does consist of dentine: he was even inclined to consider that this layer was a special form of bone. That he arrived at such an opinion is due to an error of mine, when in the monograph of the Spitsbergen forms I mistook the pores of the mucous canals for branches from the sub-epidermal vascular plexus. Since I am able to show convincingly in the British Cephalaspids that these pores have nothing to do with the vascular canals of the exoskeleton, there is no reason to doubt any longer that the superficial layer of the exoskeleton of Cephalaspids does consist mainly of true dentine (*cf.* pp. 17–19, 71–72).

DISTRIBUTION.

As noted in the Preface, only the information written on the original labels as to formation and locality of the specimens is given in the Systematic Description and Explanation of Plates. In this chapter supplementary details are given, wherever possible, of the horizons and localities at which the Cephalaspids were found.

As most of the specimens described in this monograph were collected long before any of the recent detailed investigations on the stratigraphy of the Lower Old Red Sandstone and the underlying " Passage Beds " (see W. W. King, 1925) were carried out, the stratigraphical information on the original labels, which is largely confined to the terms " Passage Beds " and " Lower Old Red Sandstone," is of little use as judged by modern zonal standards, and unless the locality is exactly stated, definite correlation is often exceedingly difficult.

Unfortunately, the geographical information on the labels is often very vague, for in a number of cases the name of the nearest town or large village, which may be three or four miles distant, is given instead of that of the actual locality; and even when this is known, it frequently happens that several quarries occur close together, showing a considerable range of strata. In such circumstances the only means of identifying the horizons of the specimens is by comparison of their matrices with those of known age or with the rocks themselves in the field. This work, involving no little trouble and travelling to and fro, was kindly undertaken by Mr. W. Wickham King, on whose notes the following information is almost entirely based.

STRATIGRAPHY AND LOCAL FAUNAS.

In the following lists the Cephalaspid fauna of each locality is given. The number in parentheses following the name of the locality is in each case the approximate horizon according to the classification of Mr. Wickham King (1925, pp. 383–384).

A. GREY + RED DOWNTONIAN (Ludlow Bone-bed—I. 10).*

Shropshire.

Ludlow (L. B. B.)—*Sclerodus pustuliferus.*
Ludlow (" Passage Beds " I. 2)—*Hemicyclaspis murchisoni, H. m.* var. *ludlowensis, H. lightbodii, Thyestes salteri.*
Norton (L. B. B.)—*Sclerodus pustuliferus.*

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* The various localities in Ayrshire and Lanarkshire from which *Ateleaspis tessellata* (*q.v.* p. 150) has been recorded cannot as yet be correlated with the English Downtonian areas and are not recorded here.

Herefordshire.

Downton Bridge (I. 1)—*Sclerodus pustuliferus.*
Kington (I. 1)—*Sclerodus pustuliferus.*
Ledbury (" Passage Beds " I. 2)—*Hemicyclaspis murchisoni, H. m.* var. *ludlowensis, H. lightbodii, Thyestes egertoni, Didymaspis grindrodi, Sclerodus pustuliferus.*
Bush Pitch (I. 7)—*Didymaspis grindrodi.*
*Ammons Hill (I. 9)—*Didymaspis grindrodi.*

Staffordshire.

Baggeridge Colliery (I. 2)—*Hemicyclaspis murchisoni, Sclerodus pustuliferus.*
*Ellowes Park (I. 2)—*Hemicyclaspis murchisoni, Didymaspis grindrodi.*
*Holly Bank Colliery (I. 2)—*Hemicyclaspis murchisoni.*

Worcestershire.

Man Brook, Trimpley (I. 6)—*Didymaspis grindrodi.*
*Stanford Clay-pit (I. 7)—*Didymaspis grindrodi.*

B. DITTONIAN (II. 1–3).

Shropshire.

Downton Hall (II. 2)—*Cephalaspis whitei, C. fletti.*
Whitbach (II. 1)—*Cephalaspis whitei, C. lankesteri, C. agassizi, C. whitbachensis,* (?) *C.* sp. nov.

N.B.—There are several quarries and smaller exposures near Whitbach, ranging in zone from I. 8 to II. 2, but the matrix of the British Museum fossils is that of the fine-grained reddish and greenish mottled cornstones and sandstones of zone II. 1 exposed in two quarries, the better of which, on the east side of the road to Whitbach Hill, contains beds said by Marston (1870, *A Guide to the Ferns . . . round Ludlow,* etc., p. 26) to have been " very productive."

Ludlow, near (? II. 1–2)—*Cephalaspis acutirostris, C. agassizi.*

N.B.—The exact localities of these specimens are unknown, but the matrices are similar to those of certain specimens from Downton Hall and Whitbach, especially from the former.

Herefordshire.

Cradley (II. 1)—*Cephalaspis salweyi, C. agassizi,* (?) *C. fletti, C. cradleyensis,* (?) *C. langi, C. sollasi, Benneviaspis lankesteri, B. anglica.*

N.B.—These specimens apparently came from the pits near Ridgeway Farm, which are in zone II. 1, and not from the large quarry in zone I. 9 at Ridgeway Cross, a mile to the south-east.

Leverhill (II. 1)—*Cephalaspis fletti, Benneviaspis anglica, Securiaspis kingi.*
Whyle Rock (II. 3)—*Cephalaspis whitei.*
Kentchurch Hill (II. 3)—*Securiaspis kitchini.*
Pontrilas, near (II. ? 3)—*Cephalaspis whitei, C. langi.*

N.B.—The exact locality or localities of these specimens are not certain. The matrix of the specimens of *C. whitei* (Brit. Mus. nos. P. 7167, P. 7168*a*), a deep red cornstone lightly mottled with green, resembles certain beds (II. 3) in Corras quarry, Kentchurch, 2½ miles S.E. of Pontrilas, and also somewhat earlier rocks (II. ? 2) from Coldharbour Farm quarry, 1 mile E. of Pontrilas.

* These additional localities are included here on the authority of Mr. W. Wickham King.

Worcestershire.

Guildings Brook, Trimpley (II. 1)—*Cephalaspis fletti.*
Heightington (II. 3)—*Cephalaspis salweyi,* (?) *C. whitei, C. heightingtonensis.*
Acton Beauchamp (II. 3)—*Cephalaspis salweyi.*

Monmouthshire.

Skirrid Fawr (II. 1)—*Cephalaspis salweyi, C. agassizi, Securiaspis kitchini.*
Asylum Grounds, Abergavenny (II. ?)—*Cephalaspis woodwardi.*

N.B.—The specimens, like those of *Pteraspis crouchi* found here, are apparently out of the drift. The native rock at this locality is not younger than I. 8, but the matrix of these specimens, a mottled green and red cornstone, is very different and resembles rather bands in the lowest quarry (II. ?) on the south end of Deri.

LOWER OLD RED SANDSTONE (not zoned).

The strata of the Scottish localities cannot be exactly correlated with those of the Anglo-Welsh area, but all seem to be younger than the Downtonian, except perhaps those of Oban and the Isle of Kerrera, which Mr. Wickham King suggests may be Downtonian, like the Stonehaven area. The Forfarshire localities are described by G. Hickling (1912), who gives a list which includes places, unnoted in this monograph, where *Cephalaspis lyelli* is said to have been found: these records must be discounted until the specimens have been re-examined.

Argyllshire.

Oban—*Cephalaspis lornensis.*
I. of Kerrera—*Cephalaspis lornensis.*

Forfarshire.

Leysmill—(?) *Hemicyclaspis* sp.
Turin Hill—*Cephalaspis pagei, C. spinifer, C. powriei* var. *brevicornis, C. p.* var. *asper.*
Pitairlie—*Cephalaspis pagei.*
Tealing—*Cephalaspis pagei.*
Reswallie—*Cephalaspis pagei.*
Carmylie—*Cephalaspis pagei.*
Brechin—*Cephalaspis powriei* typica, (?) *C. lyelli.*
Middleton—(?) *Cephalaspis powriei* typica.
Kinblythmont—*Cephalaspis powriei* var. *brevicornis.*
Glammis—*Cephalaspis lyelli,* (?) *C.* sp. nov.
Aberlemno—*Cephalaspis* sp.
Sidlaw (*sic*)—*Cephalaspis* sp.

Perthshire.

Rossie Priory—*Cephalaspis powriei* var. *brevicornis, C. watsoni.*

Ayrshire.

Tulloch Quarry, Galston Moor—*Cephalaspis traquairi.*

LOWER DEVONIAN (not zoned).

Cornwall.

Looe—“ *Steganodictyum* ” *carteri.*
Lantivet Bay—“ *Steganodictyum* ” *carteri.*

N.B.—These beds are of *post*-Dittonian age.

MIDDLE OLD RED SANDSTONE.

Caithness.

Spital—*Cephalaspis magnifica.*

DISTRIBUTION OF SPECIES.

In the following section, the full list of localities is given under each fossil, and is followed by the approximate range.

Hemicyclaspis murchisoni *
- Ludlow
- Ledbury
- Baggeridge Colliery
- †Ellowes Park
- †Holly Bank Colliery

Range : I. 2.

H. m. ludlowensis
- Ludlow
- Ledbury

Range : I. 2.

H. lightbodii
- Ludlow
- Ledbury

Range : I. 2.

Cephalaspis salweyi
- Cradley
- Heightington
- Skirrid Fawr
- Acton Beauchamp

Range : II. 1–3.

C. whitei
- Whitbach
- Downton Hall
- Whyle Rock
- Pontrilas (near)
- ? Heightington

Range : II. 1–3.

C. heightingtonensis
- Heightington

Range : II. 3.

C. acutirostris
- Ludlow (near)

Range : II. 1 or 2 ?

C. lankesteri
- Whitbach

Range : II. 1.

C. agassizi
- Whitbach
- Cradley
- Ludlow (near)
- Skirrid Fawr

Range : II. 1.

* This species is also recorded from the Downtonian of Norway (J. Kiaer, 1931).
† See footnote, p. 200.

C. fletti
Cradley
Downton Hall
Leverhill
Guildings Brook, Trimpley
Range : II. 1–2.

C. cradleyensis
Cradley
Range : II. 1.

C. whitbachensis
Whitbach
Range : II. 1.

C. langi
Pontrilas (near)
? Cradley
Range : II. 1–3 ?

C. sollasi
Cradley
Range : II. 1.

C. woodwardi
Asylum Grounds, Abergavenny
Range : II. ?

C. pagei
Turin Hill
Pitairlie
Tealing
Reswallie
Carmylie
Range : II. or higher.

C. spinifer
Turin Hill
Range : II. or higher.

C. powriei typica
Brechin
? Middleton
Range : II. or higher.

C. powriei brevicornis
Turin Hill
Kinblythmont
Rossie Priory
Range : II. or higher.

C. powriei asper
Turin Hill
Range : II. or higher.

C. traquairi
Tulloch Quarry, Galston Moor
Range : I. or II.

C. lornensis
Oban
I. of Kerrera
Range : ? I.

C. lyelli
Glammis
? Brechin
Range : II. or higher.

C. watsoni
Rossie Priory
Range : II. or higher.

C. magnifica
Spital
Range : M.O.R.S.

Benneviaspis lankesteri
Cradley
Range : II. 1.

B. anglica
Cradley
Leverhill
Range : II. 1.

Securiaspis kitchini
Kentchurch Hill
Skirrid Fawr
Range : II. 1–3.

S. kingi
Leverhill
Range : II. 1.

Thyestes salteri
Ludlow
Range : I. 2.

Thyestes egertoni
Ledbury
Range : I. 2.

Didymaspis grindrodi
Ledbury
Bush Pitch
Man Brook, Trimpley
*Ellowes Park
*Ammons Hill
*Stanford Clay-pit
Range : I. 2–9.

Sclerodus pustuliferus
Ludlow
Ledbury
Norton
Kington
Downton Bridge
Baggeridge Colliery
Range : L.B.B.—I. 2.

" *Steganodictyum* " *carteri*
Looe
Lantivet
Range : *Post*–II.

* See footnote, p. 200.

SUMMARY.

The researches carried out on the British Cephalaspids have greatly added to our knowledge of the Cephalaspids in general, especially in regard to the general characters and squamation of the trunk, the development of the fins and the micro-structure of the exoskeleton.

Briefly summarized the most important results gained from these researches are as follows :—

1. In the superficial parts of the corium on the head, trunk and pectoral fins there was in all Cephalaspids, except probably *Sclerodus* [*Eukeraspis*], as in the Tremataspids, a system of special canals, the mucous canal system, which opened outwards by means of numerous pores. This canal system was either a slime-producing organ or a special sensory organ, the nature of which cannot be ascertained. Where the exoskeleton was present in the corium, this system was either enclosed in, or lay more or less completely superficially to it. In such places, therefore, we find this system represented in the fossils either by closed canals in the exoskeleton or by more or less distinct grooves on the external surface of the exoskeleton. In a great many cases, however, it was even situated entirely superficially to the exoskeleton, so that it gave rise to neither grooves nor other markings on the external surface.

2. The mucous canal system was arranged so as to form a network. This network, when typically developed, was in the form of wide meshes within which were finer meshes. The areas of the exoskeleton situated within the wide meshes are often very conspicuous, and it is these which, on account of their shape, were termed polygonal areas in the work on the Spitsbergen Cephalaspids. Thus it was the mucous canal system that caused the subdivision of the exoskeleton into polygonal areas.

3. The mucous canal system greatly influenced the arrangement of the vessels of the corium. In the exoskeleton it is clearly seen that the vessels of the corium were arranged in vascular areas or polygons which coincide with the polygonal areas of the exoskeleton. Thus it is obvious that the very peculiar structure of the exoskeleton of the Cephalaspids as a whole is due to the presence of the mucous canal system.

4. The exoskeleton of the Cephalaspids is subject to considerable variations in the development of its outer layers, not only in different species, but even in different specimens of the same species.

5. The squamation of the trunk presents certain Anaspid-like characters, and especially noteworthy is the resemblance of the ventro-lateral processes of the ventro-lateral scales to the spines of the pectoral plate and to the post-branchial rods of the *Anaspida.*

6. A well-developed paired ventral fin-fold is present, and this represents the ventral fins of fishes.

7. In some Cephalaspids there are two well-developed dorsal fins, but in others the anterior fin is represented by a crest or spine on the cephalic shield and by a pronounced crest on the trunk immediately behind the cephalic shield. In still other forms there may be no traces whatever of an anterior dorsal fin.

8. The caudal fin, at least in *Hemicyclaspis* and *Cephalaspis*, has, in addition to its main axis, a small ventral axis supporting a separate lobe of the caudal fin-membrane. It is not unlikely that this ventral axis, with its lobe, may represent an anal fin.

9. The mouth-opening of the Cephalaspids is of a type similar to that in the Pteraspids, being slit-like and bounded on the dorsal side by a maxillary plate not infrequently armed with tooth-like tubercles, and on the ventral side by oral plates.

10. The external branchial openings seem in all Cephalaspids to be ten in number, as in *Tremataspis*.

11. The Cephalaspids show strikingly small variations in their internal structures, such as the nerves and vessels.

The recent extension of our knowledge of the Ostracoderms in general has also enabled me to discuss in detail certain points in their anatomy, especially of the Pteraspids. The most important conclusions resulting from this are as follows :—

1. The conditions in the Pteraspids with regard to the mutual relations between the mouth-opening, the olfactory organ and the naso-hypophysial opening were distinctly Myxinoid, thus strongly supporting my previous suggestion that the *Heterostraci* are closely allied to the ancestors of the Myxinoids and belong to the same branch of the Ostracoderm stem.

2. A mucous canal system homologous to that of the Cephalaspids and Tremataspids was probably present in the Pteraspids and in all the other *Heterostraci*. In the Pteraspids it was possibly situated in the grooves between, and was thus the cause of, the dentine-ridges and the form of the superficial layer of the exoskeleton ; that is, it is the presence of the mucous canal system which gave rise to the peculiar development of the superficial parts of the exoskeleton of the Pteraspids. In the Drepanaspids it was probably situated between the dentine-tubercles, and in the Coelolepids between the scales.

3. The presence of a mucous canal system, the *Petromyzon*-like arrangement of the lateral sensory canal system and the development of the mouth show that the Pteraspids, despite the fact that they were specialized in a Myxinoid direction, were certainly closely allied to the *Osteostraci*.

4 Finally, the organization of the Pteraspids shows quite clearly that the *Heterostraci* are in no way related to the Elasmobranchs, but are lowly-organized, agnathous vertebrates, and undoubtedly Ostracoderms.

LITERATURE.

ABEL, O. 1919. Die Stämme der Wirbeltiere. Berlin und Leipzig.

AGASSIZ, L. 1835. Recherches sur les Poissons fossiles, II, i, 85–200. Neuchâtel. (Pls. 1*a*, *b* were published in 1837.)

——. 1839. Fishes of the . . . Upper Silurian Rocks. In R. I. Murchison's "Silurian System," 605–607, 704. London.

——. 1844*a*. Monographie des Poissons fossiles du Vieux Grès Rouge ou Système dévonien (Old Red Sandstone) des Iles Britanniques et de Russie. Neuchâtel.

——. 1844*b*. Recherches sur les Poissons fossiles, II, ii, 73–336. Neuchâtel.

ALLIS, E. P. 1901. The Lateral Sensory Canals, the Eye-Muscles and the Peripheral Distribution of certain of the Cranial Nerves of MUSTELUS LAEVIS. *Quart. Journ. Microsc. Sci. London*, XLV, 87–236.

——. 1903. On certain Features of the Lateral Canals and Cranial Bones of POLYODON FOLIUM. *Zool. Jahrb., Jena*, Abt. Anat. XVII, 659–678.

BOLL, F. 1868. Die Lorenzini'schen Ampullen der Selachier. *Arch. mikr. Anat. Bonn*, IV, 375–391.

——. 1875. Les Vescicole di Savi della Torpedine. *Atti r. Acc. Lincei, Roma*, (2), II, 385–392.

BRAUS, H. 1904. Die Entwickelung der Form der Extremitäten und des Extremitätenskeletts. In Hertwig's "Handbuch der . . . Entwickelungslehre der Wirbeltiere," (1906), III, ii, 167–338. Jena.

BROHMER, P. 1908. Die Sinneskanäle und die Lorenzinischen Ampullen bei SPINAX-Embryonen. *Anat. Anz., Jena*, XXXII, 25–40.

BULMAN, O. M. B. 1930. On the General Morphology of the Anaspid LASANIUS Traquair. *Ann. & Mag. Nat. Hist., London*, (10), VI, 354–362.

CHAPMAN, F. 1906. New or little-known Victorian Fossils in the National Museum. Part VII. A new Cephalaspid, from the Silurian of Wombat Creek. *Proc. Roy. Soc. Victoria, Melbourne*, (n.s.) XVIII, 93–100.

——. 1914. Australasian Fossils. Melbourne.

DE BEER, G. R. 1931. Discussion "On the Relationships of the Ostracoderms to the Cyclostomes." *Proc. Linn. Soc. London*, Session 142, 50–51.

EGERTON, P. M. G. 1857. Palichthyologic Notes. No. 9. On some Fish-remains from the Neighbourhood of Ludlow. *Quart. Journ. Geol. Soc. London*, XIII, 282–291.

EICHWALD, E. VON. 1854. Die Grauwackenschichten von Liev.- und Esthland. *Bull. Soc. imp. Nat. Moscou*, XXVII, 1–111.

——. 1860. Lethaea Rossica, Vol. 1, ii. Stuttgart.

GOODRICH, E. S. 1904. On the Dermal Fin-rays of Fishes—Living and Extinct. *Quart. Journ. Microsc. Sci. London*, XLVII, 465–522.

——. 1906. Notes on the Development, Structure and Origin of the Median and Paired Fins of Fish. *Quart. Journ. Microsc. Sci. London*, L, 333–376.

——. 1908. On the Scales of Fish, Living and Extinct, and their Importance in Classification. *Proc. Zool. Soc. London*, 1907, 751–774.

——. 1909. Vertebrata Craniata. I. Cyclostomes and Fishes. In LANKESTER'S "A Treatise on Zoology," IX. London.

——. 1930. Studies on the Structure and Development of Vertebrates. London.

——. 1931. Discussion "On the Relationships of the Ostracoderms to the Cyclostomes." *Proc. Linn. Soc. London*, Session 142, 45–49.

GÖPPERT, E. 1902. Die Entwickelung des Mundes, und der Mundhöhle, etc. In HERTWIG'S "Handbuch der . . . Entwickelungslehre der Wirbeltiere," II, i (1906), 1–108. Jena.

HARLEY, J. 1859. Description of two Species of CEPHALASPIS. *Quart. Journ. Geol. Soc. London*, XV, 503–505.

HICKLING, G. 1912. (i) The Old Red Sandstone Rocks near Arbroath. (ii) On the Geology and Palæontology of Forfarshire. *Proc. Geol. Assoc., London*, XXIII, 299–311.

HUXLEY, T. H. 1858. On CEPHALASPIS and PTERASPIS. *Quart. Journ. Geol. Soc. London*, XIV, 267–280.

JAEKEL, O. 1902. Über COCCOSTEUS und die Beurtheilung der Placodermen. *Sitzungsb. Gesell. naturf. Freunde Berlin*, 1902, 103–115.

——. 1903. Über TREMATASPIS und PATTENS Ableitung der Wirbeltiere von Arthropoden. *Zeitschr. deutsch. Geol. Gesell. Berlin*, LV, Monatsber., 84–93.

——. 1911. Die Wirbeltiere. Berlin.

——. 1921. Paläontologische Berichte. II. Schädelprobleme. *Palaeont. Zeitschr., Berlin*, III, 217–239.

JOHNSTON, J. B. 1902. The Homology of the Selachian Ampullae. *Anat. Anz., Jena*, XXI, 308–313.

KIAER, J. 1915. Upper Devonian Fish Remains from Ellesmere Land with Remarks on DREPANASPIS. *Report of the Second Norwegian Arctic Expedition in the "Fram," 1898–1902*, XXXIII. *Publ. Vidensk.-Selsk. Kristiania.*

——. 1924. The Downtonian Fauna of Norway. I. Anaspida, with a Geological Introduction. *Skr. Vidensk.-Selsk. Kristiania.* I. Mat.-naturv. Kl. no. 6.

——. 1928. The Structure of the Mouth of the Oldest Known Vertebrates, Pteraspids and Cephalaspids. *Palaeobiologica, Wien*, I, 117–134.

——. 1930. CTENASPIS, a new Genus of Cyathaspidian Fishes. A Preliminary Report. *Norg. Svalb.-Ishavs-Undersøk.—Skrifter om Svalbard og Ishavet, Oslo*, XXXIII.

——. 1931. HEMICYCLASPIS MURCHISONI-faunaen i. den downtoniske Sandsten på Jeløen i Oslofjorden. *Norsk geol. Tidsskr., Oslo*, XII, 419–433.

KING, W. W. 1925. Notes on the "Old Red Sandstone" of Shropshire. *Proc. Geol. Assoc., London*, XXXVI, 383–389.

KOKEN, E. 1911. Pisces. In ZITTEL'S "Grundzüge der Paläontologie." II. Aufl. 2, 1–142. München & Berlin.

KUPFFER, C. VON. 1899. Zur Kopfentwicklung von BDELLOSTOMA. *Sitzungsb. Gesell. Morph. Physiol. München*, XV, 21–35.

——. 1900. Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten. 4. Zur Kopfentwicklung von BDELLOSTOMA. München & Leipzig.

LANKESTER, E. R. 1867. On DIDYMASPIS, a new Genus of Cephalaspidian Fishes. *Geol. Mag., London*, IV, 152–154.

——. 1870. A Monograph of the Fishes of the Old Red Sandstone of Britain. Part I. The CEPHALASPIDAE. *Palaeontogr. Soc., London.*

LERICHE, M. 1906. Contributions à l'Étude des Poissons fossiles du Nord de la France et des Régions voisines. *Mém. Soc. géol. Nord, Lille*, V.

MACKIE, S. J. 1861. CEPHALASPIS from Old Red Sandstone near Ludlow. *Geologist, London*, IV, 141 (Edit. note).

McCOY, F. 1851. On some new Devonian Fossils. *Ann. & Mag. Nat. Hist., London*, (2), VIII, 481–490.

——. 1852. British Palaeozoic Rocks and . . . Fossils. Part II. Palaeontology. London & Cambridge.

MERKEL, F. 1880. Über die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere. Rostock.

MILLER, H. 1841. The Old Red Sandstone; or New Walks in an Old Field. 1st Ed. Edinburgh.

MINCKERT, W. 1901. Zur Topographie und Entwickelungsgeschichte der Lorenzinischen Ampullen. *Anat. Anz., Jena*, XIX, 497–528.

MURCHISON, R. I. 1839. The Silurian System. Part II. London.

——. 1867. Siluria. 4th ed. London.

PANDER, C. H. 1856. Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements. St. Petersburg.

PATTEN, W. 1903*a*. On the Structure of the PTERASPIDAE and CEPHALASPIDAE. *Amer. Naturalist, Boston*, XXXVII, 827–865.

PATTEN, W. 1903*b*. On the Structure and Classification of the TREMATASPIDAE. *Mém. Acad. imp. Sci. St. Pétersbourg,* (8), XIII, v.

——. 1912. The Evolution of the Vertebrates and their Kin. Philadelphia & London.

POWRIE, J. 1861. Cephalaspides of Forfarshire. *Geologist, London,* IV, 137–140.

RAYMOND, P. E. 1925. The ANASPIDA and the Problem of the Origin of the Vertebrates. *Amer. Journ. Sci., New Haven,* (5), X, 433–436.

RETZIUS, G. 1898. Zur Kenntniss der Lorenzinischen Ampullen der Selachier. *Biol. Untersuch., Stockholm,* n.F. VIII, 75–82.

ROHON, J. V. 1892. Die obersilurischen Fische von Oesel. I. THYESTIDAE und TREMATASPIDAE. *Mém. Acad. imp. Sci. St. Pétersbourg,* (7), XXXVIII, xiii.

——. 1893. Die obersilurischen Fische von Oesel. II. SELACHII, DIPNOI, GANOIDEI, PTERASPIDAE, und CEPHALASPIDAE. *Mém. Acad. imp. Sci. St. Pétersbourg,* (7), XLI, v.

——. 1895. Die Segmentirung am Primordialcranium der obersilurischen Thyestiden. *Verh. russ.-kais. min. Gesell. St. Petersburg,* (2), XXXIII, 17–64.

——. 1896. Weitere Mittheilungen über die Gattung THYESTES. *Bull. Acad. imp. Sci. St. Pétersbourg,* (5), IV, ii, 223–235.

——. 1897. Beiträge zur Classification der palaeozoischen Fische. *Sitzungsb. kön. böhm. Gesell. Wiss., Prag,* Math.-nat. Cl., 1896, II, xxxvii.

SALTER, J. W. 1869. CEPHALASPIS ASTEROLEPIS (Harley). *Trans. Woolhope Nat. Field Club, Hereford,* 1868, 240.

SCHLOSSER, M. 1918. Pisces. In Zittel's "Grundzüge der Paläontologie," II, Aufl. 3, 5–158. München & Berlin.

——. 1923. Pisces. In Zittel's "Grundzüge der Paläontologie," II, Aufl. 4, 5–162. München & Berlin.

SCHMIDT, F. 1866. Über THYESTES VERRUCOSUS Eichw. und CEPHALASPIS SCHRENKII Pand., nebst einer Einleitung über das Vorkommen silurischer Fischreste auf der Insel Oesel. *Verh. russ.-kais. min. Gesell. St. Petersburg,* (2), I, 217–250.

——. 1894. Über CEPHALASPIS (THYESTES) SCHRENCKI Pand. aus dem Obersilur von Rotziküll auf Oesel. *Bull. Acad. imp. Sci. St. Pétersbourg,* n.s. IV (xxxvi), 383–390.

SEWERTZOFF, A. N. 1928. Einige Bermerkungungen über die systematischen Beziehungen der ANASPIDA zu den Cyklostomen und Fischen. *Palaeont. Zeitschr., Berlin,* X, 111–125.

SIMPSON, G. G. 1926. New Reconstruction of LASANIUS. *Bull. Geol. Soc. America, New York,* XXXVII, 397–402.

SOLLAS, W. J. 1903. A Method for the Investigation of Fossils by Serial Sections. *Phil. Trans. Roy. Soc. London,* B, CXCVI, 259–263.

STENSIÖ, E. 1925*a*. On the Head of the Macropetalichthyids, etc. *Field Mus. Nat. Hist., Chicago,* Publ. 232 (Geol. Ser. IV, iv), 87–197.

——. 1925*b*. Triassic Fishes from Spitsbergen. Part II. *K. Sv. Vetensk.-Akad. Handl., Stockholm,* (3), II, i.

——. 1926. On the Sensory Canals of PTERASPIS and PALAEASPIS. *K. Sv. Vetensk.-Akad. Ark. Zool., Stockholm,* XVIIIA, xix.

——. 1927. The Downtonian and Devonian Vertebrates of Spitsbergen. Fam. CEPHALASPIDAE. *Skrifter om Svalbard og Nordishavet. Resultater av de norske statsunderstøttede Spitsbergenekspeditioner,* XII. *Norske Vidensk.-Akad. Oslo.*

STETSON, H. C. 1927. LASANIUS and the Problem of Vertebrate Origin. *Journ. Geol., Chicago,* XXXV, 247–263.

——. 1928*a*. A Restoration of the Anaspid BIRKENIA ELEGANS Traquair. *Journ. Geol., Chicago,* XXXVI, 458–470.

——. 1928*b*. A new American THELODUS. *Amer. Journ. Sci., New Haven,* XVI, 221–231.

——. 1931. Studies on the Morphology of the HETEROSTRACI. *Journ. Geol., Chicago,* XXXIX, 141–154.

STROMER, E. 1912. Lehrbuch der Paläozoologie, II. Leipzig & Berlin.

——. 1926. Weitere Bemerkungen über die ältesten bekannten Wirbeltier-Reste, besonders über die ANASPIDA. *Sitzungsb. bay. Akad. Wiss., München,* Math.-nat. Abt., 1926, 83–104.

——. 1930. Neues über die ältesten und primitivsten Wirbeltiere, besonders die ANASPIDA. *Sitzungsb. bay. Akad. Wiss., München,* Math.-nat. Abt., 1930, 107–121.

TRAQUAIR, R. H. 1893. On the Discovery of CEPHALASPIS in the Caithness Flags. *Ann. Scot. Nat. Hist., Edinburgh,* 1893, 206–207.

TRAQUAIR, R. H. 1894. On CEPHALASPIS MAGNIFICA, a new Fossil Fish from the Caithness Flagstones. *Proc. Roy. Phys. Soc. Edinburgh.*, XII, 269–273.

——. 1898. Summary of Progress . . . for 1897, 82–83. *Mem. Geol. Surv. U.K.*

——. 1899*a*. On a new Species of CEPHALASPIS discovered by the Geological Survey of Scotland, in the Old Red Sandstone of Oban. *Trans. Roy. Soc. Edinburgh,* XXXIX, 591–594.

——. 1899*b*. Report on Fossil Fishes collected by the Geological Survey of Scotland in the Silurian Rocks of the South of Scotland. *Trans. Roy. Soc. Edinburgh,* XXXIX, 827–864.

——. 1905. Supplementary Report on Fossil Fishes collected by the Geological Survey of Scotland in the Upper Silurian Rocks of Scotland. *Trans. Roy. Soc. Edinburgh,* XL, 879–888.

TRETJAKOFF, D. 1929. Die schleimknorpeligen Bestandteile im Kopfskelet von AMMOCOETES. *Zeitschr. Wiss. Zool. Leipzig,* CXXXIII, 470–516.

WOODWARD, A. S. 1891. Catalogue of the Fossil Fishes in the British Museum (Nat. Hist.), II. London.

——. 1898. Outlines of Vertebrate Palaeontology. Cambridge.

——. 1901. On a Cornu of CEPHALASPIS CARTERI from the Lower Devonian of Looe. *Trans. Roy. Geol. Soc. Cornwall,* XII, 431–433.

——. 1902. Fishes. In Zittel's " Text-Book of Palaeontology," Engl. Edit., trans. and edit. by C. R. Eastman, II, 1–114. London.

——. 1906. The Study of Fossil Fishes. *Proc. Geol. Assoc., London,* XIX, 266–282.

——. 1921. Presidential Address, 1920. *Proc. Linn. Soc. London.* Session 132 (1919–1920), 25–34.

WOODWARD, H. 1881. Note on a fine Head-shield of ZENASPIS (CEPHALASPIS) SALWEYI, Egerton sp. = CEPHALASPIS ASTEROLEPIS (Harley). *Geol. Mag., London,* (2), VIII, 193–194.

ZITTEL, K. A. VON. 1887. Handbuch der Palaeontologie. Abt. I. Palaeozoologie. III. PISCES, AMPHIBIA, REPTILIA, AVES., München & Leipzig.

——. 1895. Grundzüge der Palaeontologie (Palaeozoologie). München & Leipzig.

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EXPLANATION OF PLATES

For photographing the specimens here figured panchromatic plates alone have been used (" Ilford " special rapid panchromatic). The photographs of low magnification have been taken with Zeiss' " Tessar " objectives 1 : 6·3, F. 36 cm. or 1 : 6·3, F. 25 cm., whereas for those taken at greater magnifications Zeiss' " Microplanar " and apochromatic microscopic objectives were used. As it was often desirable to obtain the finest detail and in addition strong contrasts in colour between the skeletal remains and the matrix, it was necessary to photograph the specimens in fluids of suitable refractive indices. In this way it was possible to obtain excellent results even with specimens which, when dry, could hardly be distinguished from the rock. The fluids which gave the best results were xylol, Canada balsam diluted with xylol, oleum cedri (for blackish and dark-coloured specimens in general) and undiluted Canada balsam (for light-coloured specimens). The filters mostly used were the " Ilford " micro-filter no. 5 (for blackish and dark-coloured specimens in general) and the " Ilford Gamma " filter (for light-coloured specimens).

The term " Lower Old Red Sandstone " includes both the " Red Downtonian " and the " Dittonian " of Mr. W. Wickham King's classification of these strata (see pp. 199–202).

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PLATE 1.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Specimen wanting caudal region, left lateral view. (See also Pl. 2, fig. 1; Pl. 57, fig. 3.) Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 6023 (II)**.—G. H. Piper Coll., 1889]. Slightly enlarged.

FIG. 2.—Same specimen, dorsal view. Slightly enlarged.

FIG. 3.—Part of cephalic shield of same specimen, dorsal view. × 3 diam.

dsf, dorsal electric field; *gr*, groove on lower side of pineal plate, exposed by removal of overlying bone; *ifc*, infra-orbital sensory canal-groove; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial opening (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial opening (external nasal opening proper); *orb*, orbital opening; *Pec*, pectoral fin; pin_2, pineal foramen in pineal plate; *Ppl*, pineal plate; *sclr*, sclerotic ring; sel_1, sel_2, canals of 1st and 2nd nerves of lateral electric field.

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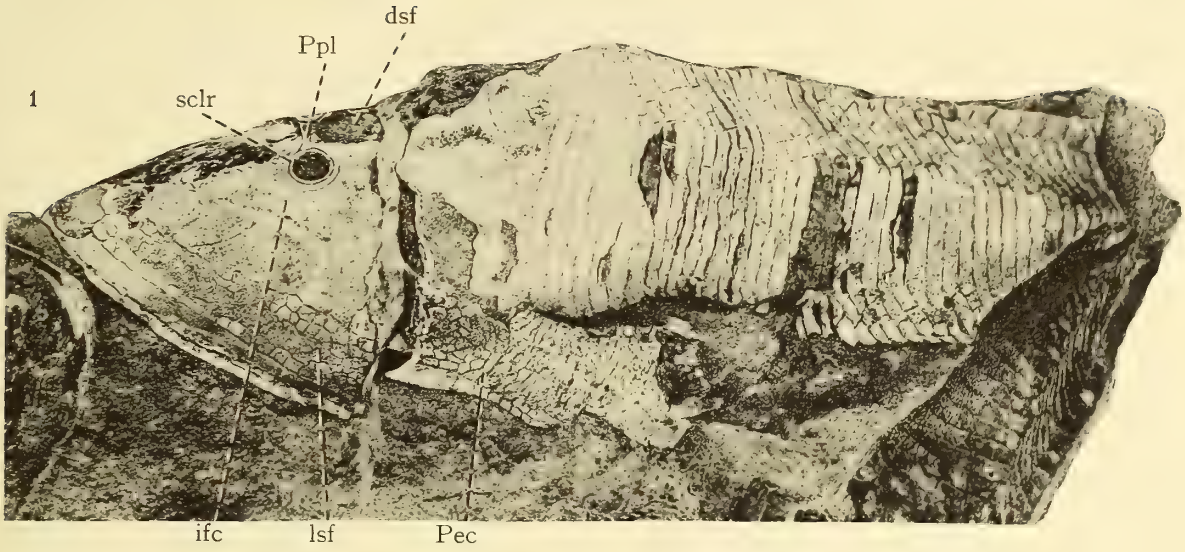

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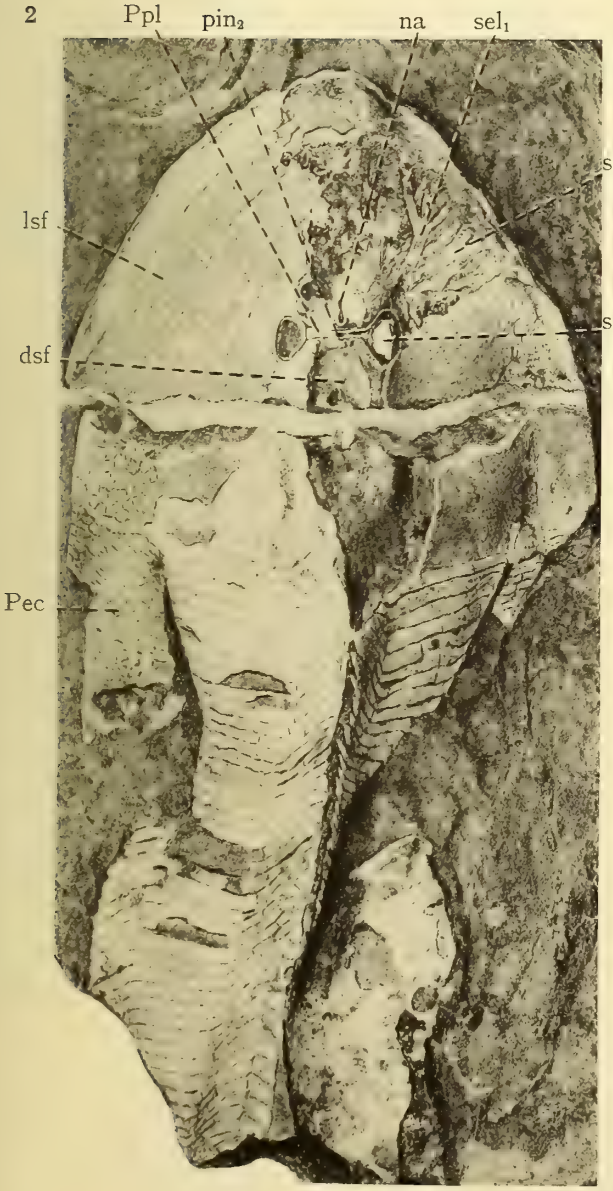

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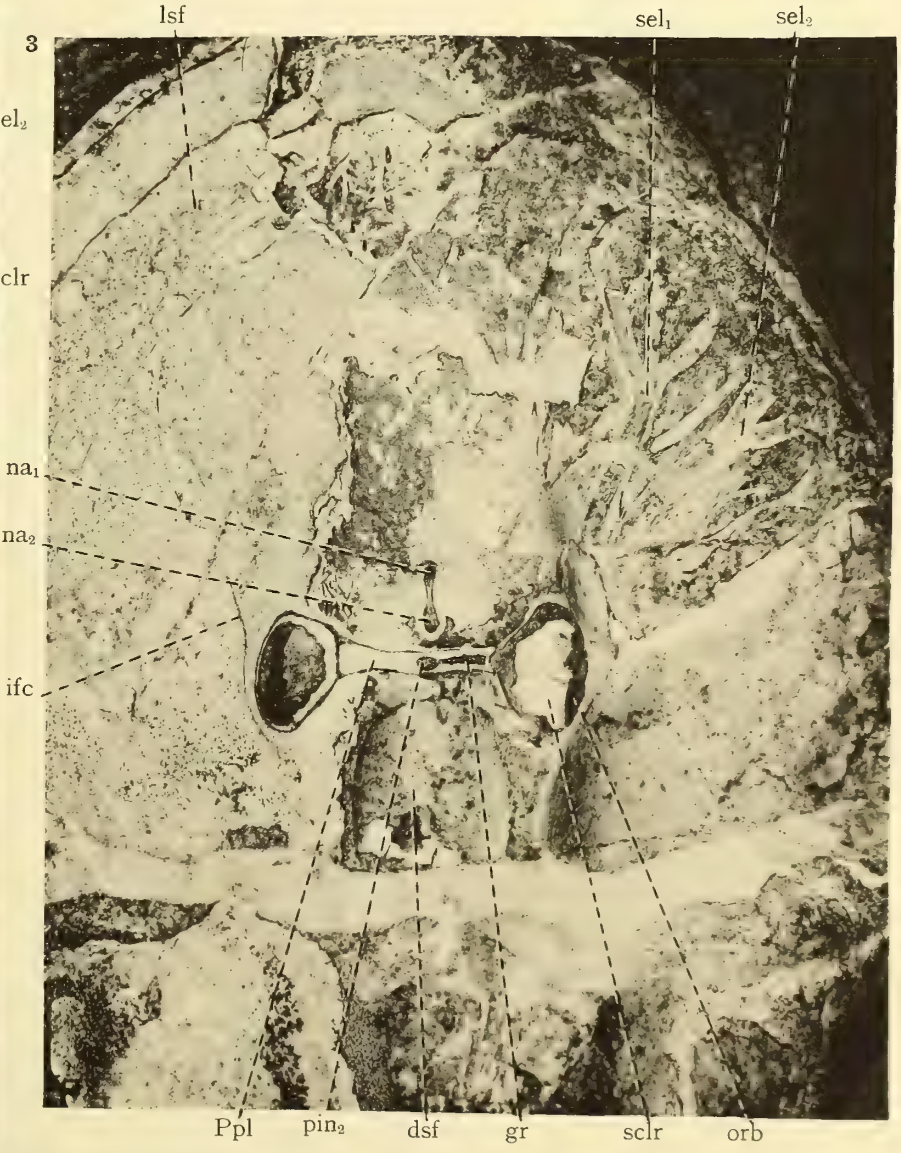

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PLATE 2.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Left pectoral fin of specimen figured in Pl. 1, dorsal view. Approx. × 4 diam.

FIG. 2.—Part of dorsal crest of trunk with adjacent squamation. Three scutes of the dorsal crest show the casts of their internal cavities (*pu*) and their mode of articulation with one another. Downtonian : loc. unknown. British Museum [no. **P. 16151.**—*ex* Coll. Hereford Museum, 1932]. Approx. × 3 diam.

FIG. 3.—*Ditto*. Approx. × 6 diam.

FIG. 4.—Almost complete specimen, dorsal view. Head-shields of two other specimens are to be seen on either side of the caudal region. (See also Pl. 3, fig. 4; Pl. 7, fig. 4.) Downtonian : Ledbury, Herefordshire. British Museum [no. **P. 6023** (**I**).—G. H. Piper Coll., 1889]. Slightly enlarged.

art.f, articular surface on side of internal cavity of scutes of dorsal crest; *C*, caudal fin; D_2, dorsal fin; *d.cr*, dorsal crest of trunk; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *ifc*, infra-orbital sensory canal-groove; *ls*, lateral scales; *lsf*, lateral electric field; *orb*, orbital opening; *Pec*, pectoral fin; pin_2, pineal foramen in pineal plate; *Ppl*, pineal plate; *pu*, internal cavity of scutes of dorsal crest; *sclr*, sclerotic ring; *sd.cr*, scutes of dorsal crest.

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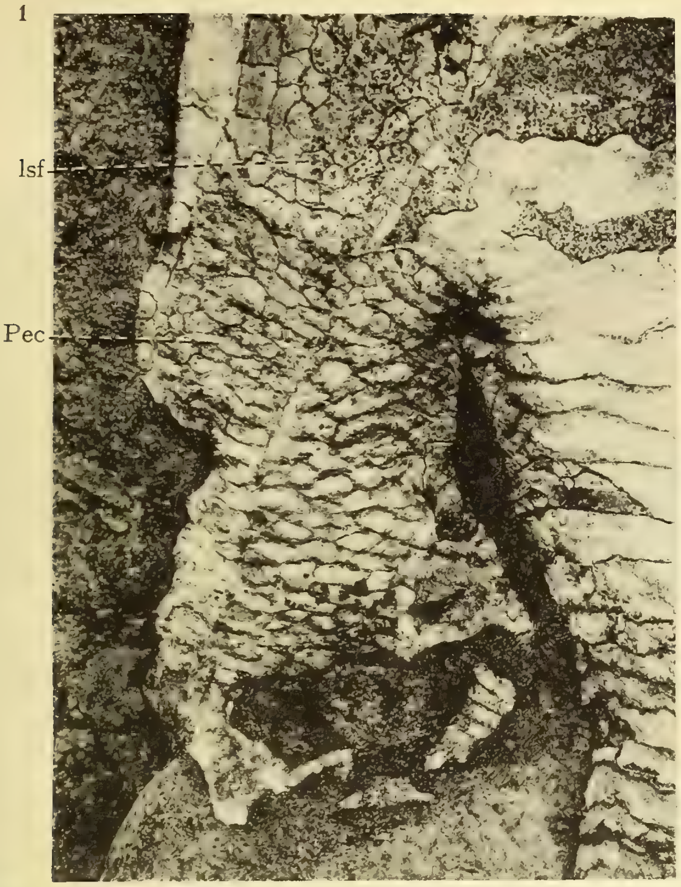

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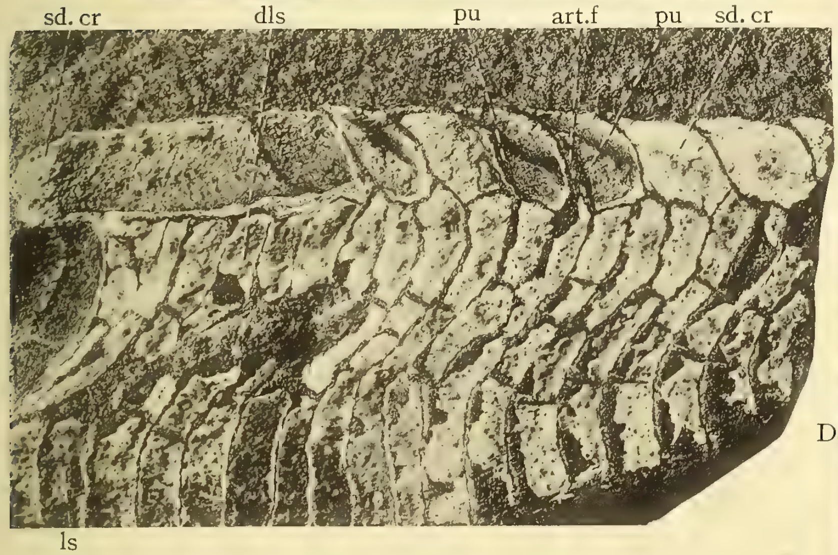

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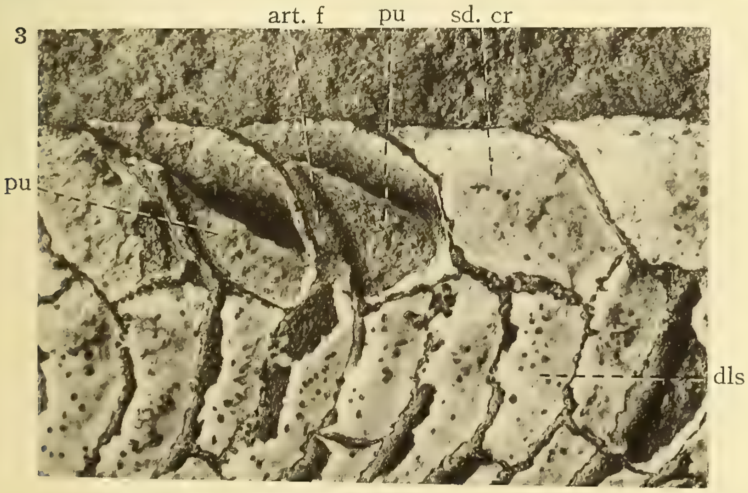

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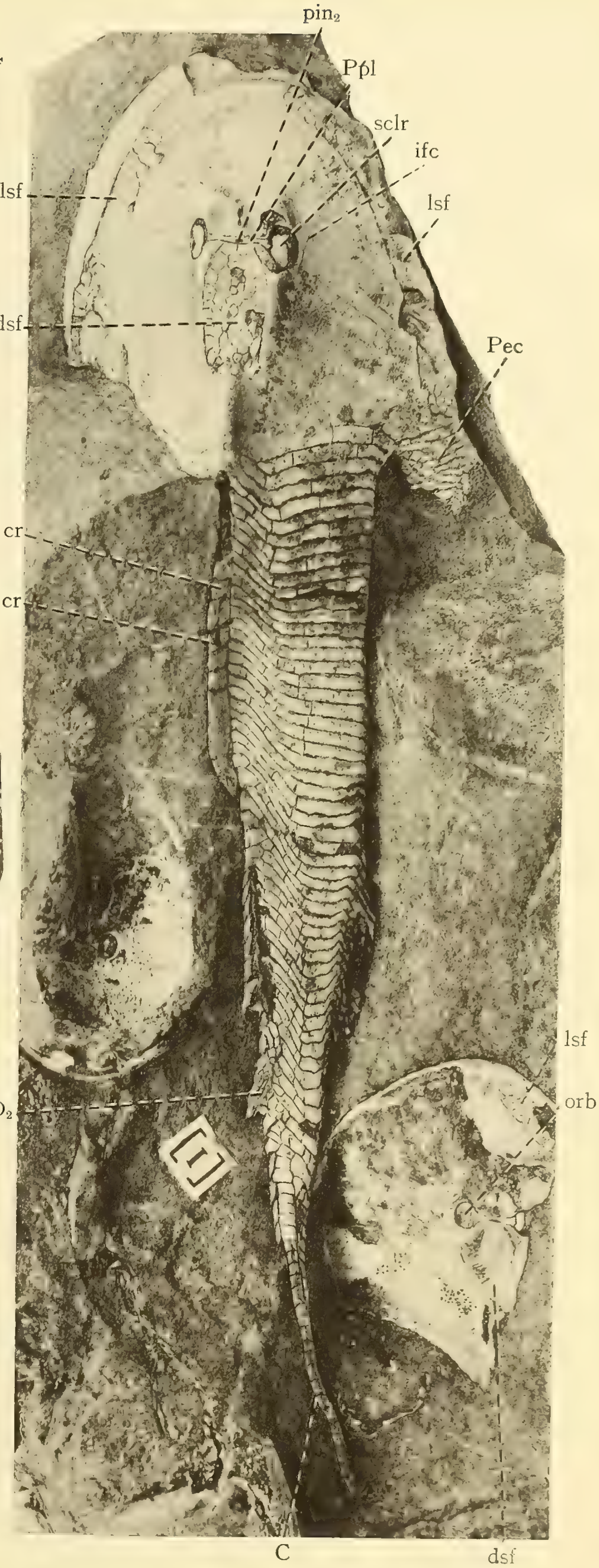

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PLATE 3.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Anterior half of specimen, from the left side. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 6261.**—G. H. Piper Coll., 1890]. Approx. × 1½ diam.

FIG. 2.—Same specimen, from the right side. Approx. × 1½ diam.

FIG. 3.—Impression of ventral surface of trunk. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8801.**—G. H. Piper Coll., 1898]. Slightly enlarged.

FIG. 4.—Almost complete specimen, lateral view. (Same specimen as in Pl. 2, fig. 4, and Pl. 7, fig. 4.) Slightly enlarged.

C, caudal fin; D_2, dorsal fin; *d.cr*, dorsal crest of trunk; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *ifc*, infra-orbital sensory canal-groove; *ls*, lateral scales; *lsf*, lateral electric field; *orb*, orbital opening; *Pec*, pectoral fin; *Ppl*, pineal plate; *sclr*, sclerotic ring; *sd.cr*, scutes of dorsal crest of trunk; *vrs*, ventro-lateral scales; *vs*, ventral scales.

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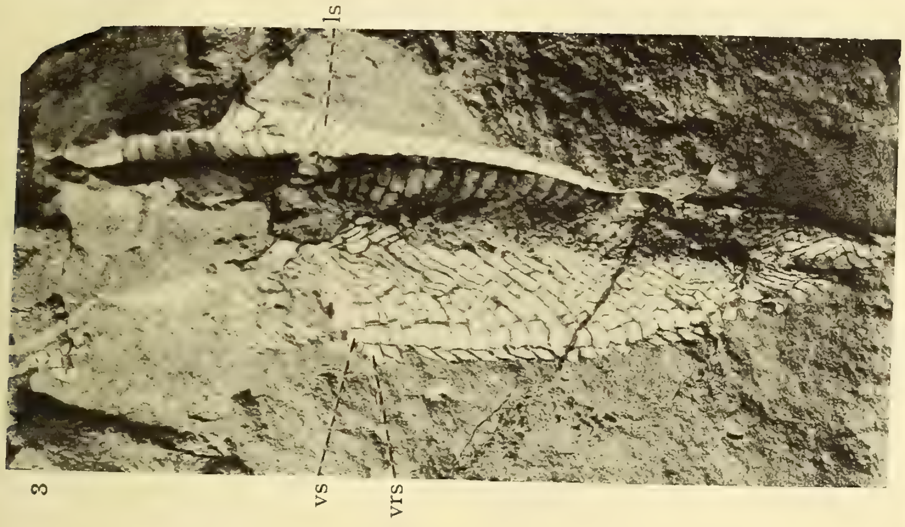

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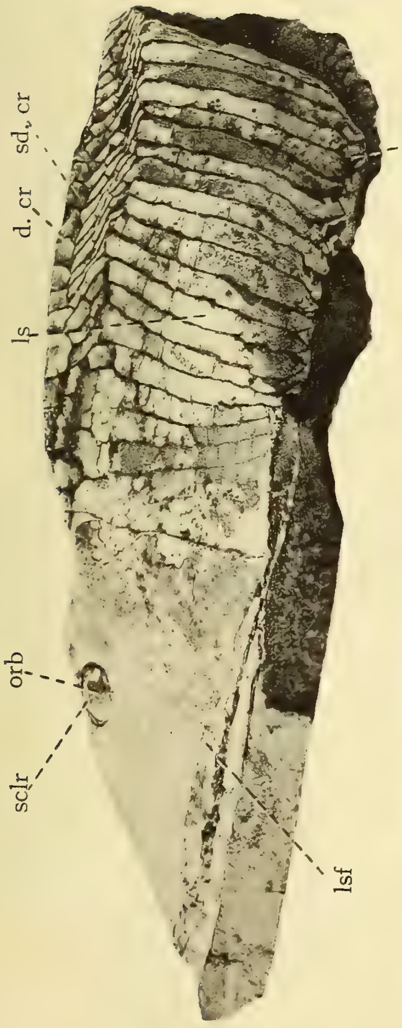

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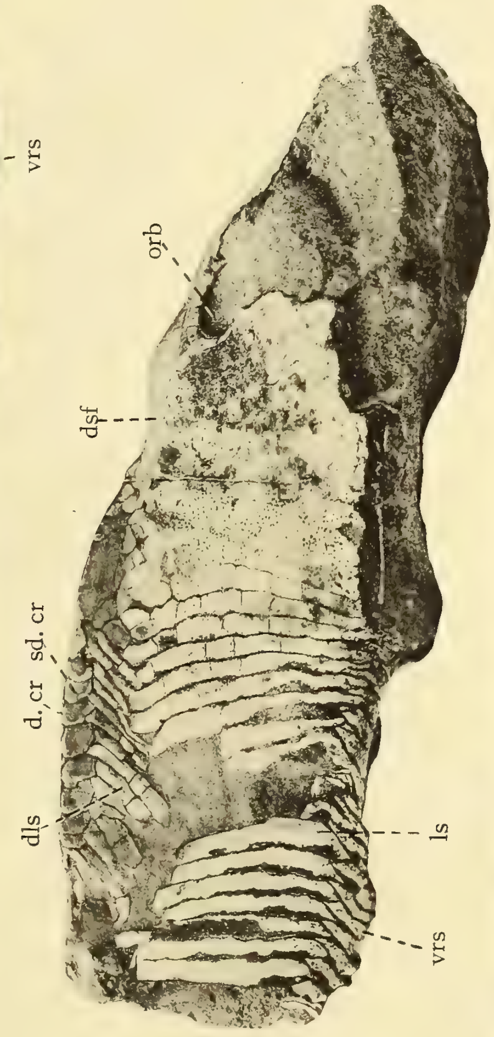

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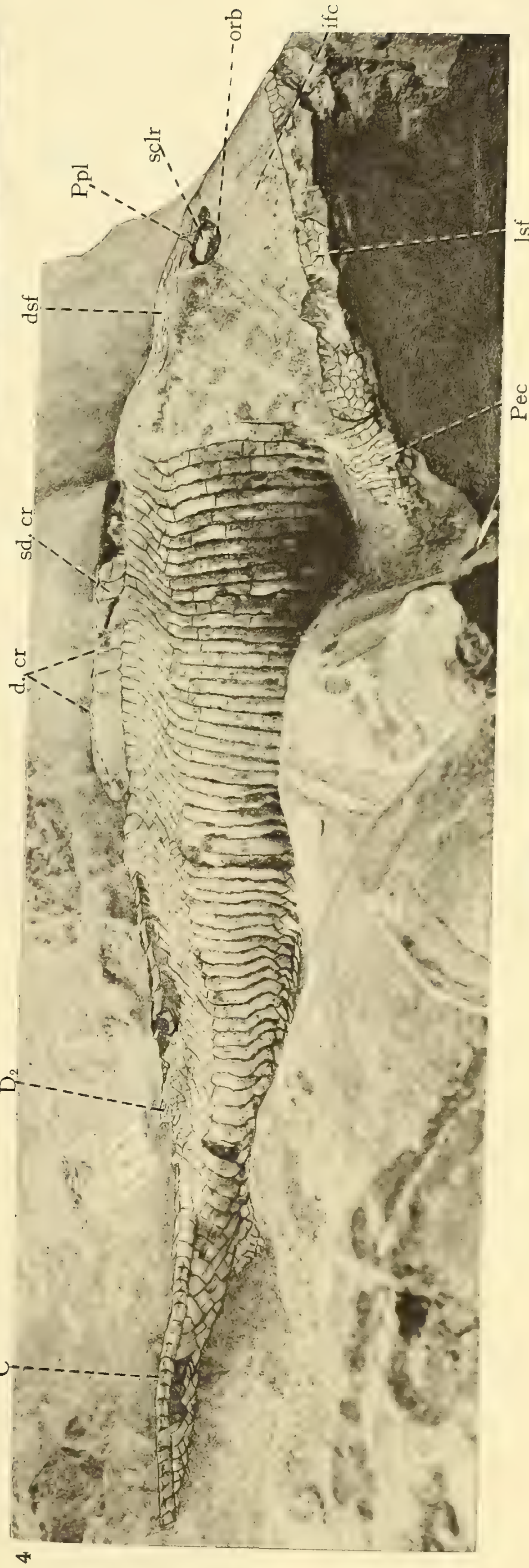

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PLATE 4.

Hemicyclaspis murchisoni (Egerton).

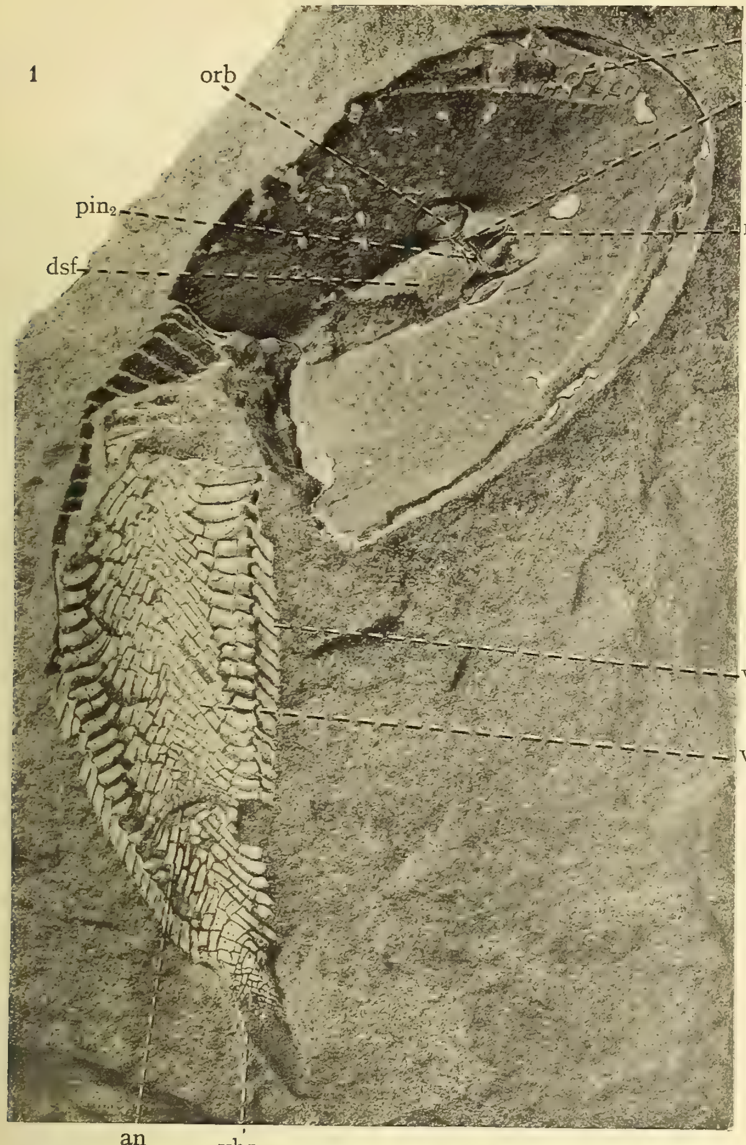
Fig. 1.—Fairly complete specimen showing the trunk in ventral view and impression of dorsal side of cephalic shield. (Counterpart of specimen in fig. 2.) Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8804.**—G. H. Piper Coll., 1898]. × 1½ diam.

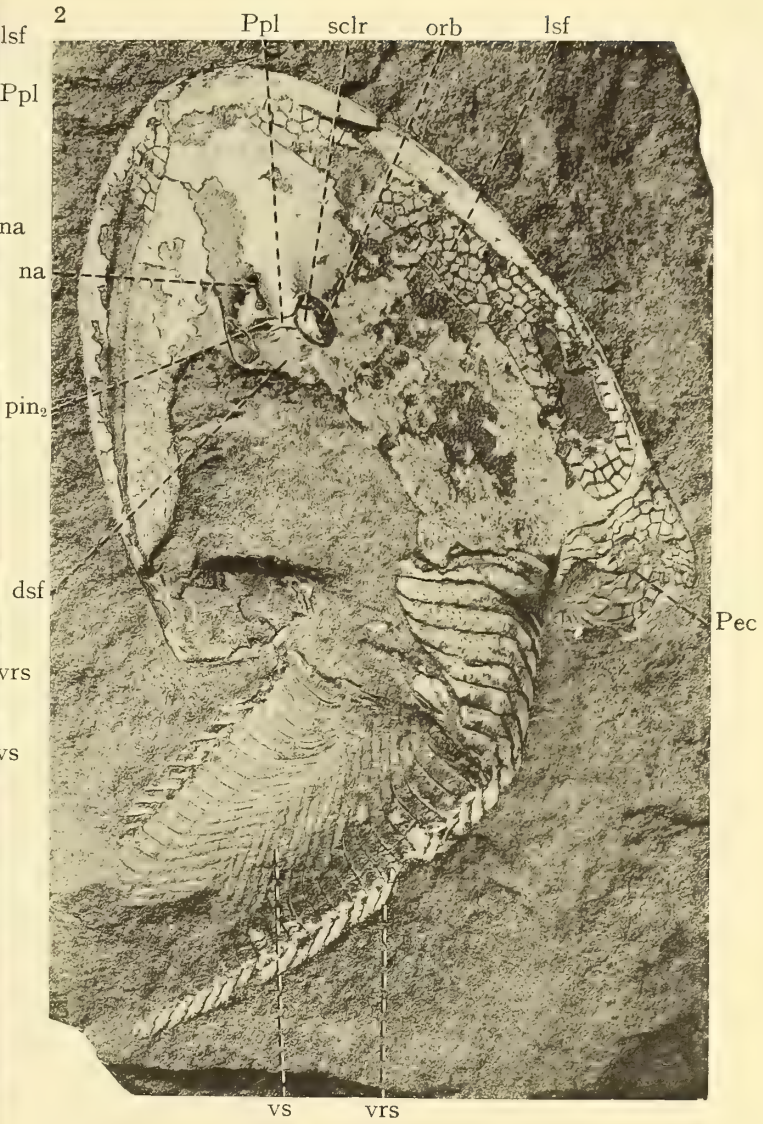
Fig. 2.—Counterpart of specimen in fig. 1. British Museum [no. **P. 6260.**—G. H. Piper Coll., 1890]. × 1½ diam.

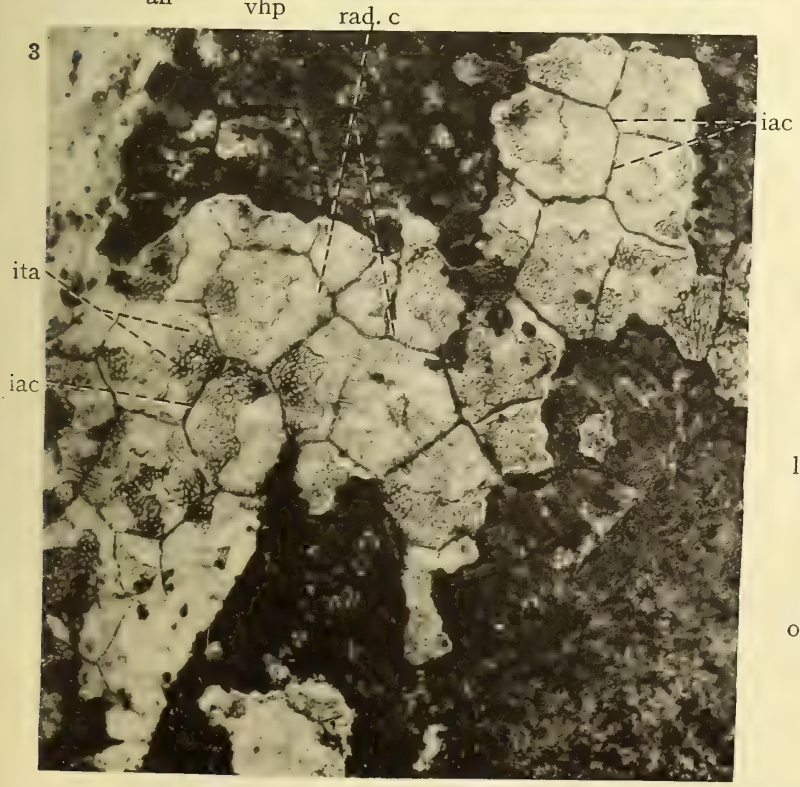
Fig. 3.—Part of inner surface of exoskeleton of cephalic shield, with mucous canal system exposed. (See also Pl. 10, fig. 2.) Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 5317(II).**—G. H. Piper Coll., 1887]. Approx. × 10 diam.

Fig. 4.—Imperfect cephalic shield, dorsal view. This specimen shows clearly some of the canals of the lateral electric field and the ornamentation of the exoskeleton. Downtonian: loc. unknown. British Museum [no. **P. 14013.**—History unknown]. × 1½ diam.

an, anal opening; *dsf*, dorsal electric field; *iac*, inter-areal mucous canals; *ita*, intra-areal mucous canals; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *Pec*, pectoral fin; pin_1, pineal opening at bottom of pineal depression; pin_2, pineal opening in pineal plate; *Ppl*, pineal plate; *rad.c*, radiating canals; *sclr*, sclerotic ring; sel_1–sel_4, canals 1–4 of nerves of lateral electric field; *vhp*, ventral axis of caudal fin; *vrs*, ventro-lateral scales; *vs*, ventral scales; V_1?, supposed canal of n. profundus.







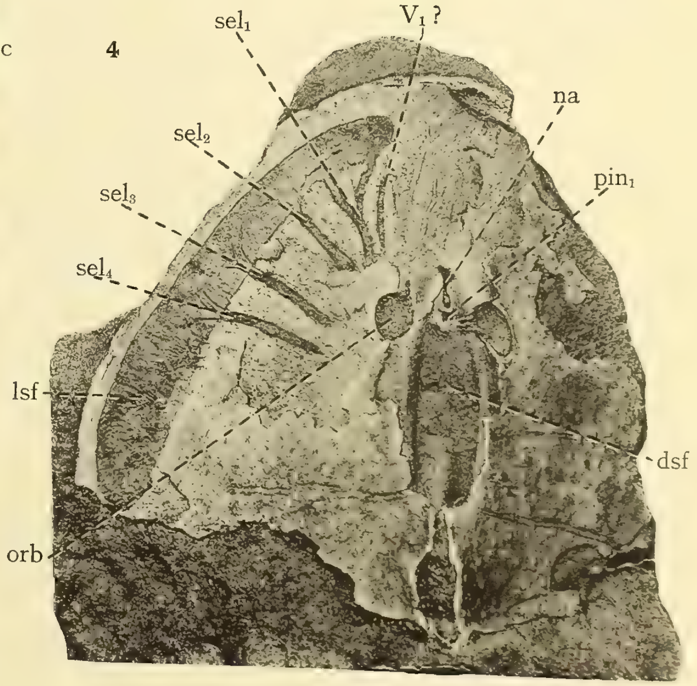


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PLATE 5.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Caudal fin from right side, showing ventral axis. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8824.**—G. H. Piper Coll., 1898]. × 2 diam.

FIG. 2.—Cephalic shield and anterior part of scale-covered division of trunk, dorso-lateral view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8803.**—G. H. Piper Coll., 1898]. × 1½ diam.

FIG. 3.—Imperfect cephalic shield with part of squamation, dorsal view. The shield shows well the exoskeletal plates of the dorsal electric field, the pineal plate and the sclerotic ring. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8809.**—G. H. Piper Coll., 1898]. × 1½ diam.

FIG. 4.—Imperfect cephalic shield with adjacent parts of squamation, dorsal view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8808.**—G. H. Piper Coll., 1898]. × 1½ diam.

FIG. 5.—Cephalic shield, dorsal view. This shield does not seem to be distorted. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8811.**—G. H. Piper Coll., 1898]. Nat. size.

FIG. 6.—Part of lateral electric field with exoskeletal plates covering it. (See also Pl. 8, fig. 3; Pl. 65, figs. 2, 3.) Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 5317(I).**—G. H. Piper Coll., 1887]. Approx. × 10 diam.

bl, basal layer of exoskeleton; *c.asc,* ascending vascular canals of basal layer; *c.sem.ant,* division of labyrinth cavity for canalis semicircularis anterior; *c.sem.post,* division of labyrinth cavity for canalis semicircularis posterior; *dsf,* dorsal electric field; *lsf,* lateral electric field; *ml,* middle layer of exoskeleton; *na,* naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial sac (nasal opening proper); *orb,* orbital opening; pin_2, pineal opening in pineal plate; *Ppl,* pineal plate; *rad.c,* radiating canals of middle layer of exoskeleton; *sclr,* sclerotic ring; sel_1–sel_4, sel_6, canals of nerves 1–4 and 6 of lateral electric field; *sl,* superficial layer; *vhp,* ventral axis of caudal fin.

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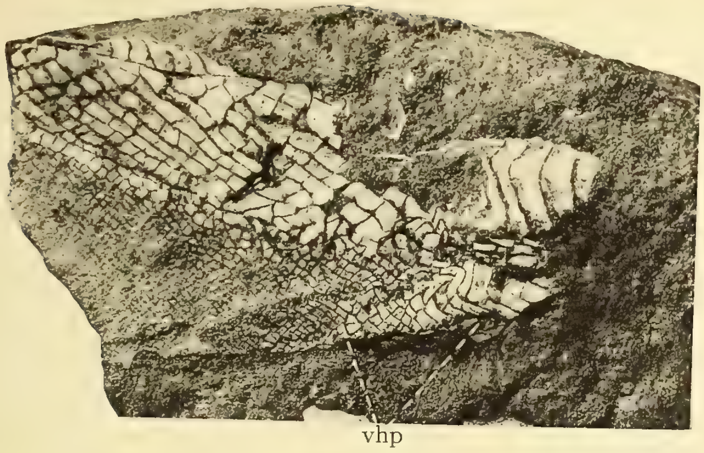

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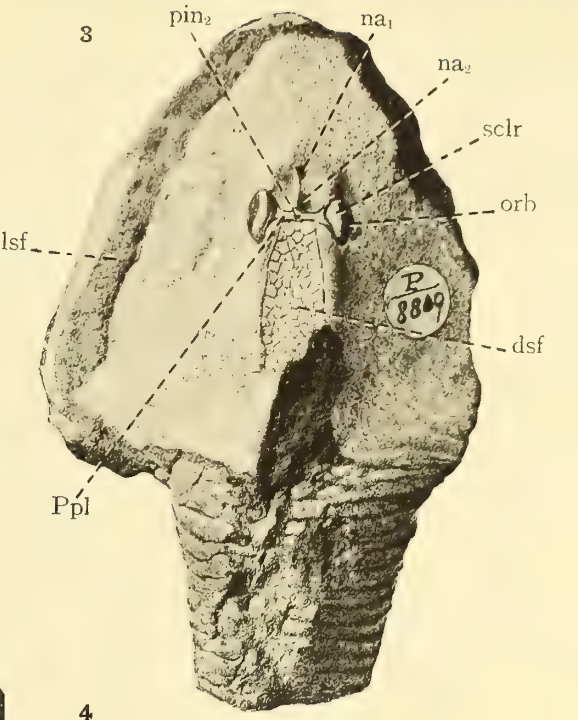

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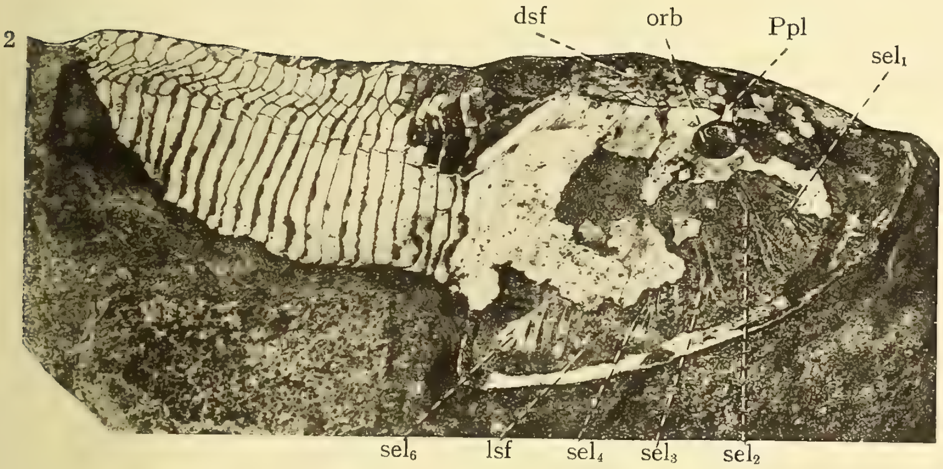

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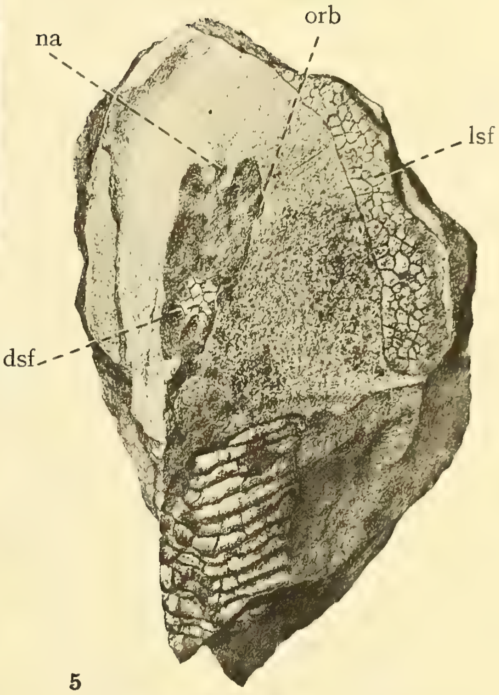

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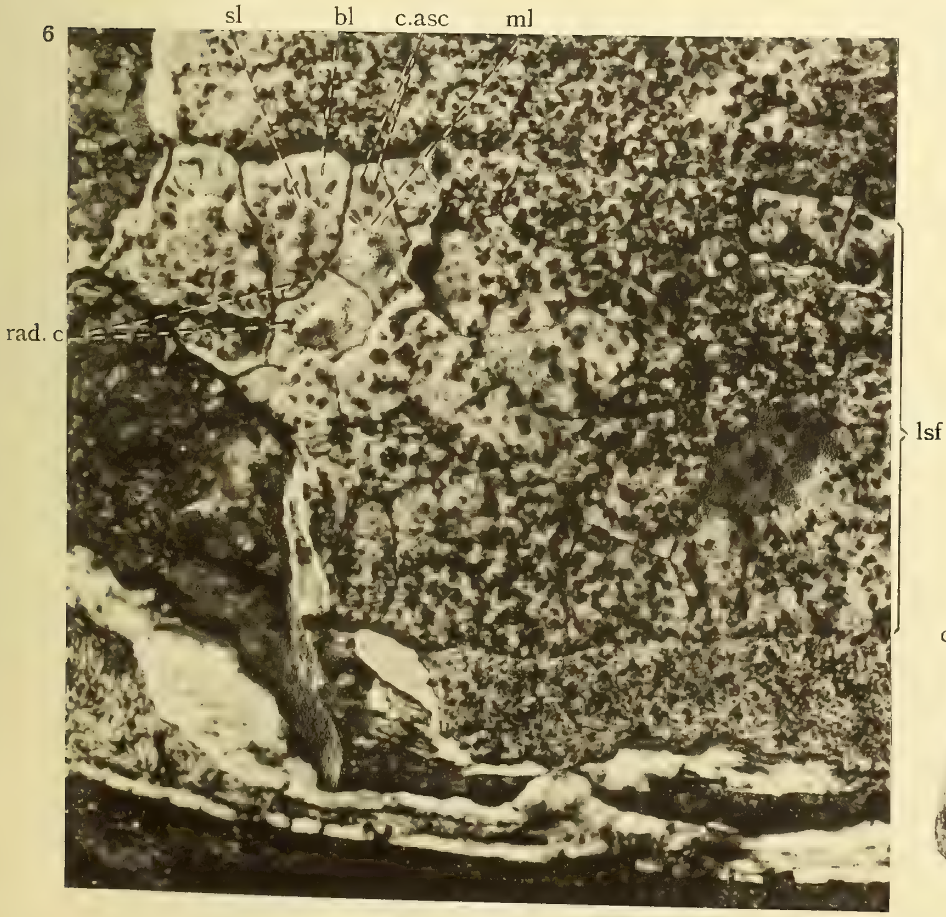

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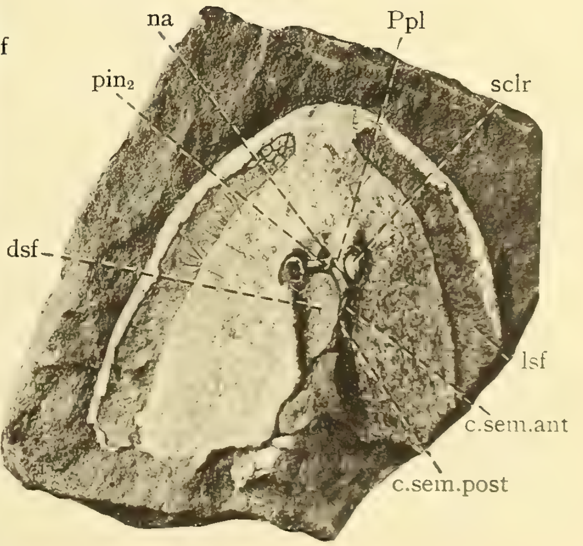

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PLATE 6.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Postero-lateral part of cephalic shield with part of ventral visceral exoskeleton and squamation of trunk, ventral view. (Partial counterpart of specimen in fig. 2.) Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8818.**—G. H. Piper Coll., 1898]. × 3 diam.

FIG. 2.—Cephalic shield showing ventral visceral exoskeleton, dorsal view. (Counterpart of specimen in fig. 1.) British Museum [no. **P. 6108.**—G. H. Piper Coll., 1889]. × 3 diam.

FIG. 3.—Left half of cephalic shield with visceral exoskeleton, ventral view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8806.**—G. H. Piper Coll., 1898]. × 3 diam.

c.asc, ascending canals of basal layer of exoskeleton; *ibs*, inter-branchial septa; *k*, external openings of branchial fossae; *lsf*, lateral electric field; *ps*, pectoral sinus; *vs*, ventral scales.

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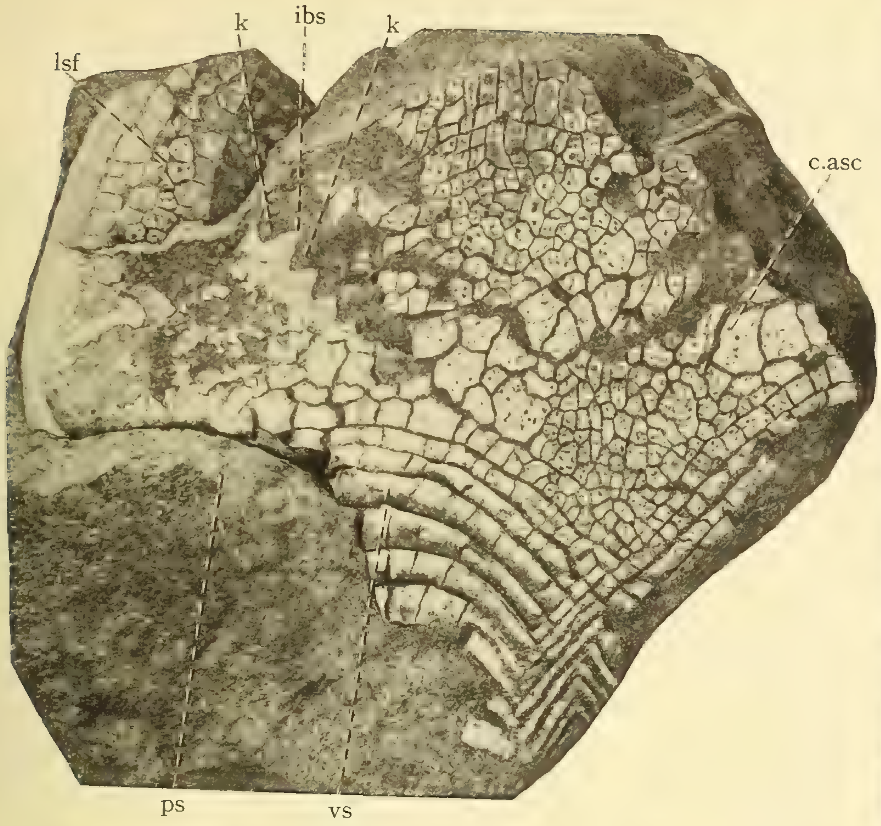

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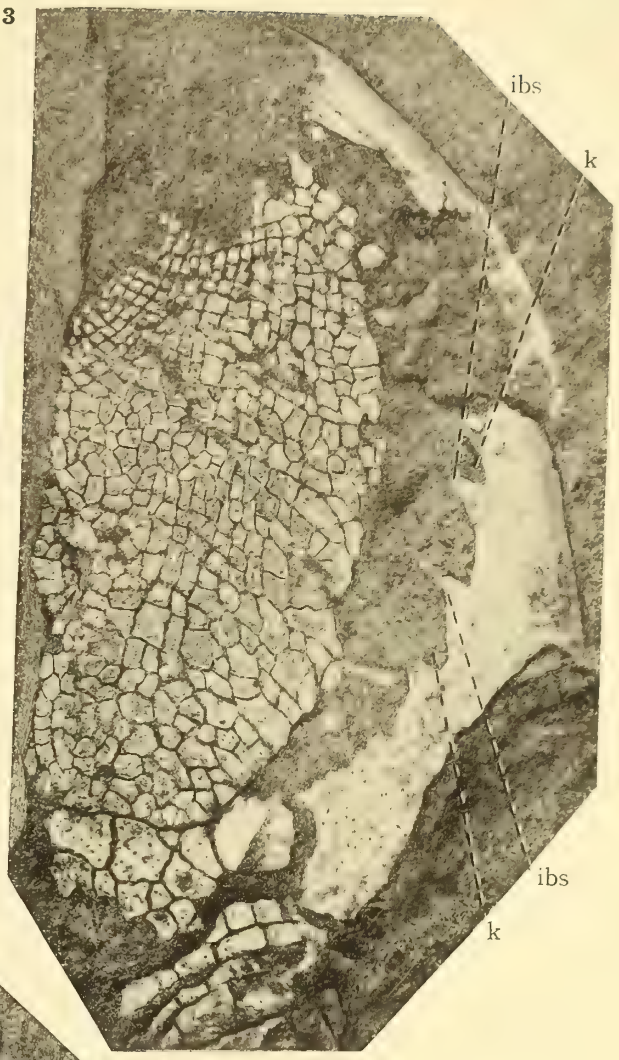

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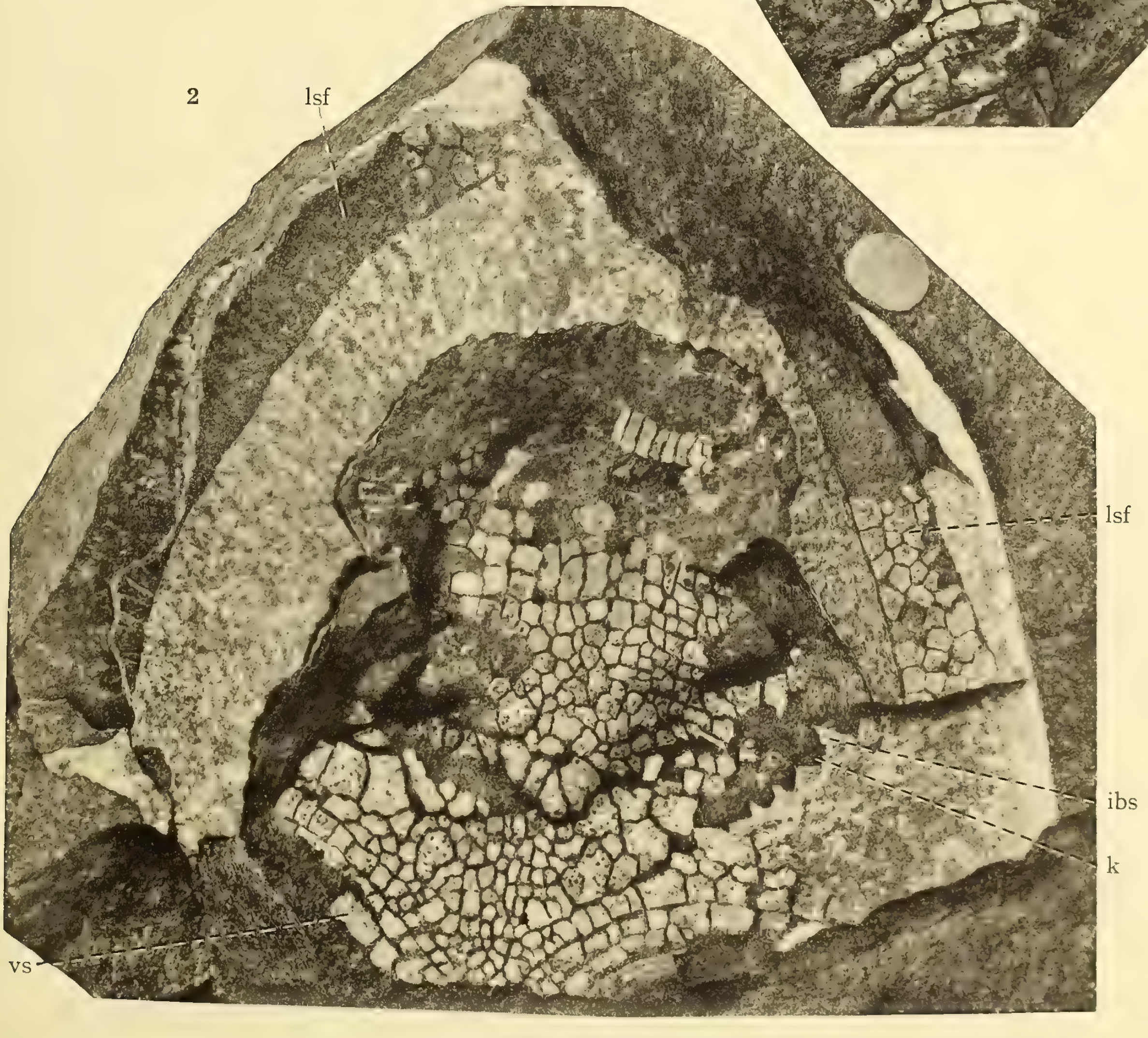

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PLATE 7.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Anterior part of scale-covered division of trunk, lateral view. Downtonian: loc. unknown. British Museum [no. **P. 14015***a*.—History unknown]. × 3 diam.

FIG. 2.—Cephalic shield, lateral view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8803***a*.—G. H. Piper Coll., 1898]. Nat. size.

FIG. 3.—Postero-lateral part of cephalic shield with squamation, ventral view. A part of the ventral visceral exoskeleton is well displayed. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8816**.—G. H. Piper Coll., 1898]. × 1½ diam.

FIG. 4.—Cephalic shield [no. **P. 6023 (III)**] and caudal region [no. **P. 6023 (I)**] of two different specimens, dorsal view. (Same specimens as in Pl. 2, fig. 4, and Pl. 3, fig. 4.) × 2½ diam.

FIG. 5.—Left half of anterior part of trunk with adjacent part of cephalic shield, ventral view. Downtonian: loc. unknown. British Museum [no. **P. 16152**.—*ex* Coll. Hereford Museum, 1932]. × 2 diam.

C, caudal fin; *ca*, covered area of lateral scale; *d.cr*, dorsal crest of cephalic shield; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *fulcr*, fulcral scales of caudal fin (dorsal ridge-scales); *ibs*, inter-branchial septa; *ls*, lateral scales; *lsf*, lateral electric field; na_1, anterior division of naso-hypophysial opening (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial opening (nasal opening proper); *obr.f*, oralo-branchial fenestra; *orb*, orbital opening; *Pec*, pectoral fin; pin_2, pineal opening in pineal plate; *Ppl*, pineal plate; *sclr*, sclerotic ring; *sel*, canal of an anterior nerve of lateral electric field; *vrs*, ventro-lateral scales; *vs*, ventral scales.

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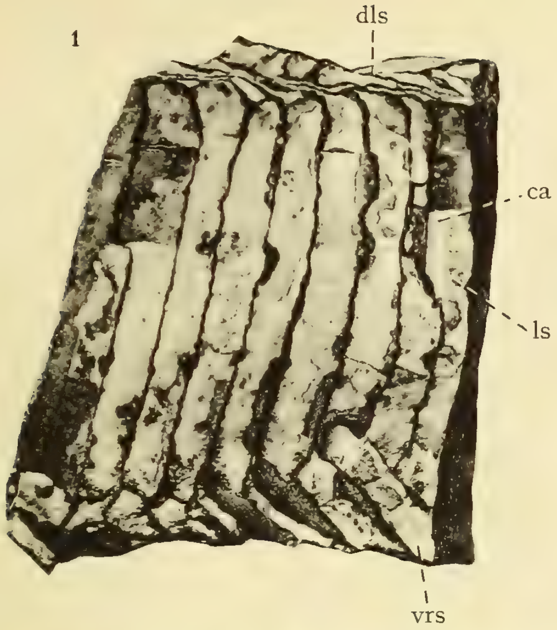

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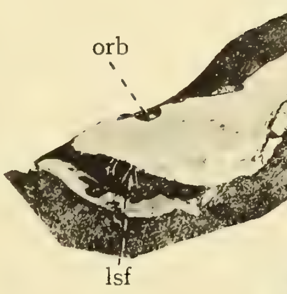

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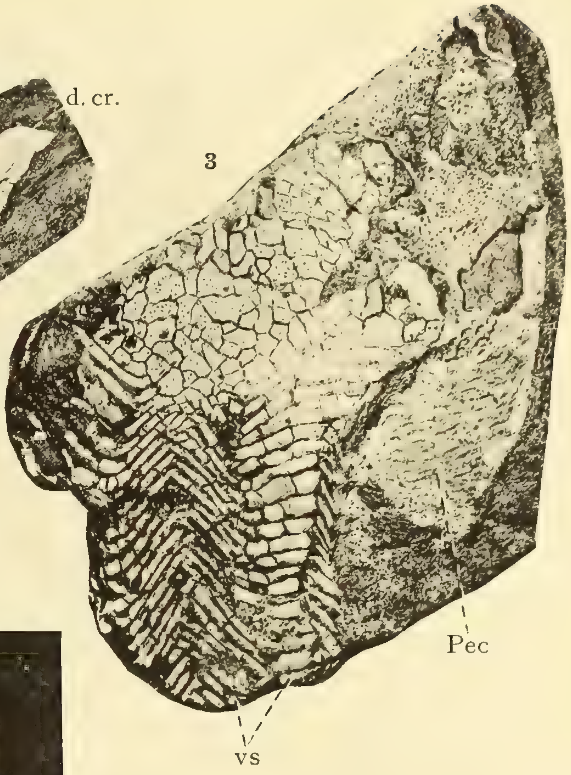

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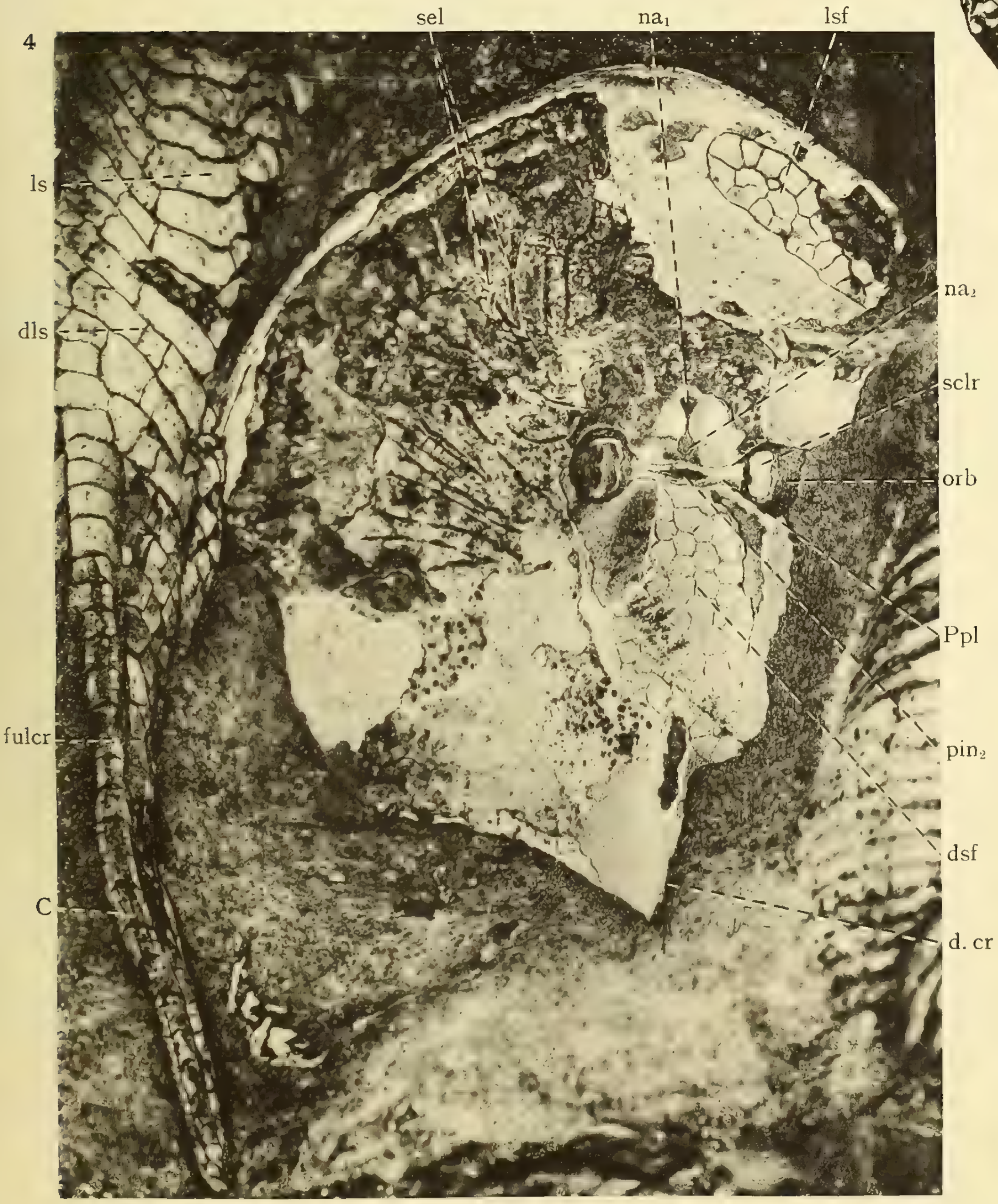

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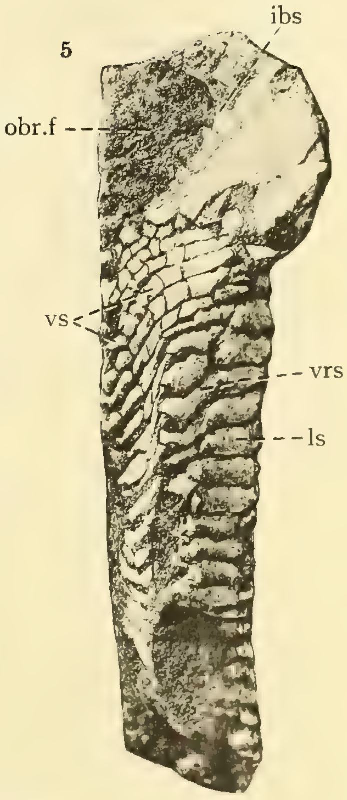

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PLATE 8.

(?) *Hemicyclaspis* sp.

Fig. 1.—Posterior half of a trunk resembling that of *H. murchisoni* (Egerton). The specimen is largely preserved as an external cast. Lower Old Red Sandstone : Leysmill, near Arbroath, Forfarshire. Museum of Practical Geology, London [no. **47820.**—J. Powrie Coll.]. × 1½ diam.

Hemicyclaspis murchisoni (Eg.), var. *ludlowensis* nov., or *H. lightbodii* (Lank.).

Fig. 2.—Imperfect ventral rim of cephalic shield. Downtonian : Ledbury, Herefordshire. British Museum [no. **P. 6111.**—G. H. Piper Coll., 1889]. Nat. size.

Hemicyclaspis murchisoni (Egerton).

Fig. 3.—Anterior part of right pectoral fin, showing squamation (part of specimen figured in Pl. 5, fig. 6, and Pl. 65, figs. 2, 3). × 10 diam.

Fig. 4.—Impressions of ventral rim and oralo-branchial chamber. This specimen is that on which Jaekel based his restoration of the " gill arches " of *H. murchisoni* (Jaekel 1903, p. 91, figs. 3, 4). Downtonian : Ledbury, Herefordshire. Geol.-Pal. Museum, of the University of Berlin [not numbered]. Approx. × 2 diam.

bl, basal layer ; D_2, dorsal fin ; *dpr*, supra-oral field (with impressions of tooth-like tubercles) ; *ibr*, inter-branchial ridge ; *ibs*, inter-branchial septum ; *k*, branchial fossae (external openings) ; *lsf*, lateral electric field ; *ml*, middle layer ; *p.brw*, post-branchial wall (perichondrial bone-layer of anterior surface) ; *pr.au*, otic prominence ; *pr.orb*, orbital prominence ; *rad.c*, radiating canals ; *sl*, superficial layer ; sel_1–sel_2, canals of 1st and 2nd nerves of lateral electric field.

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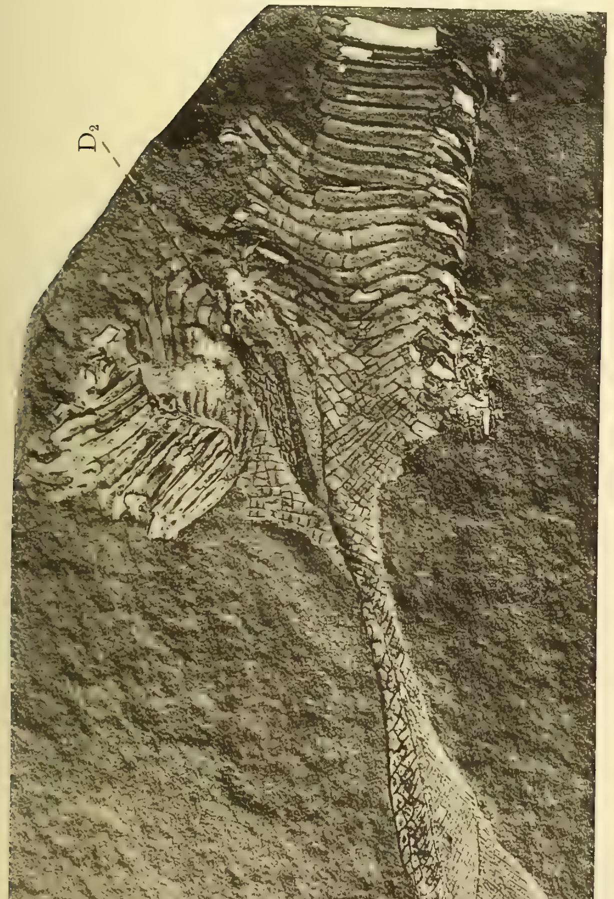

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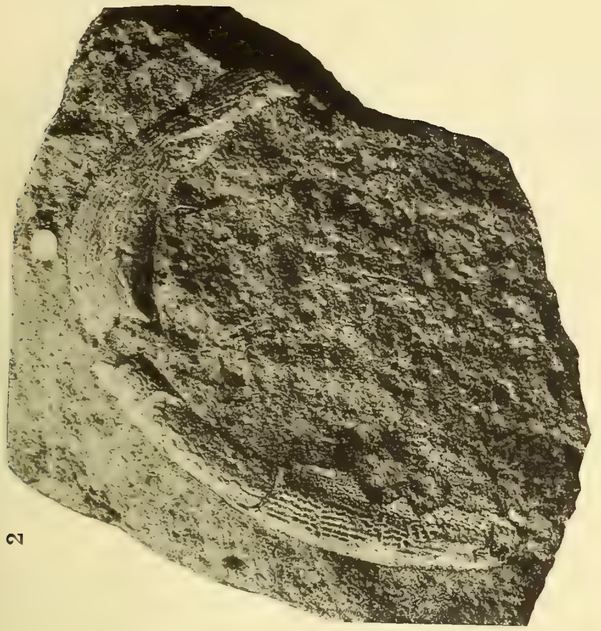

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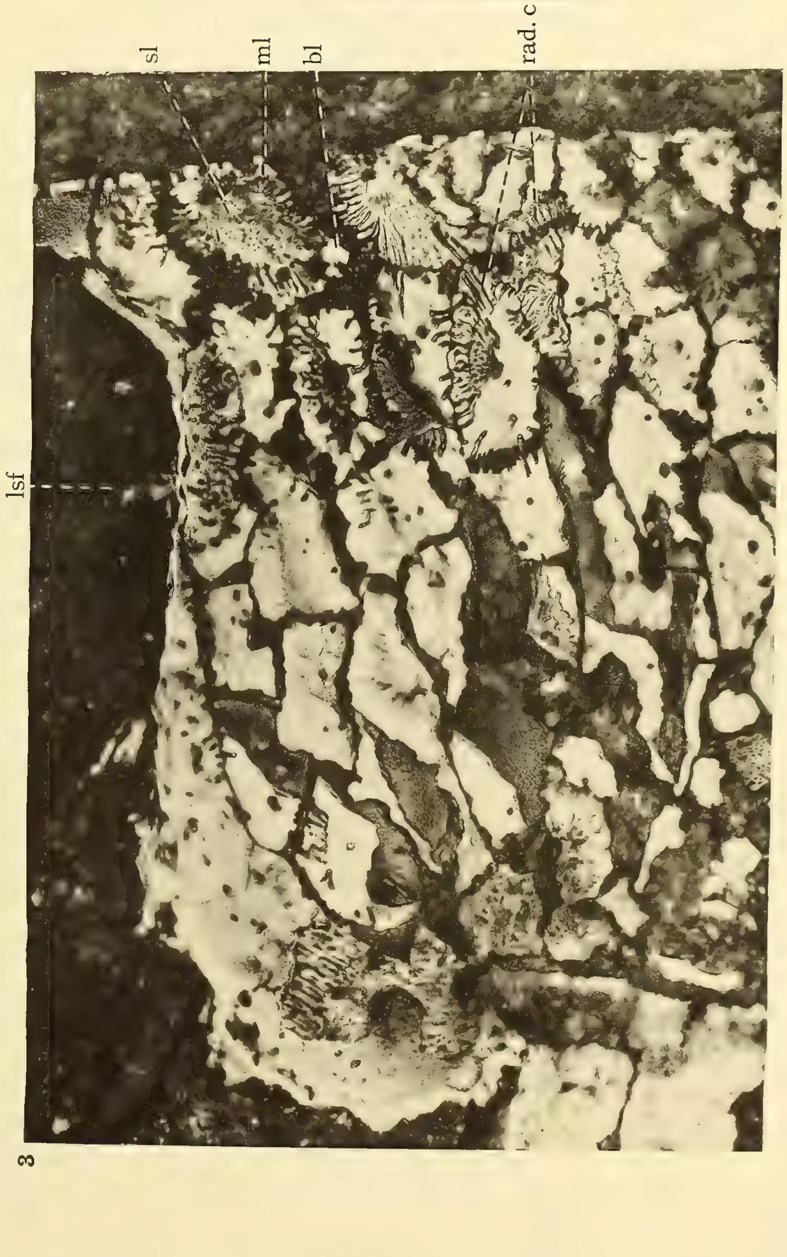

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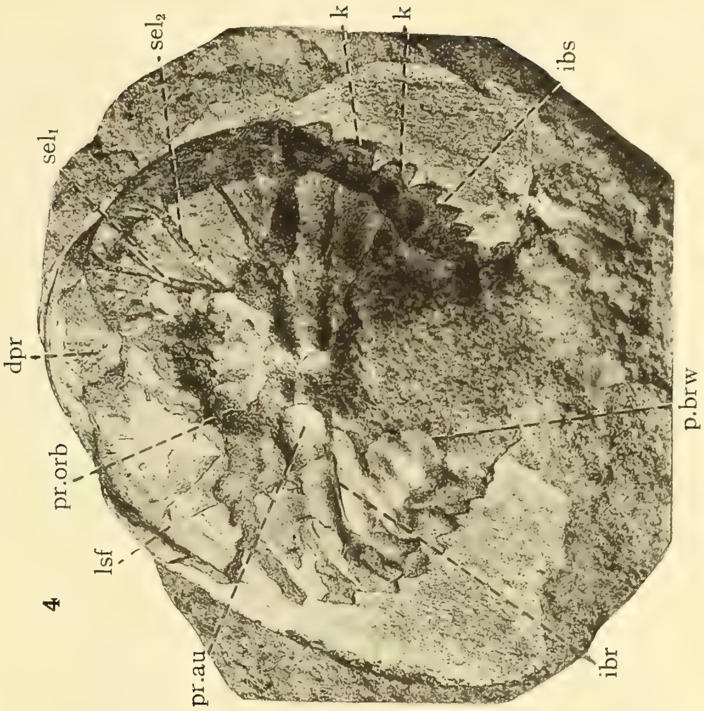

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PLATE 9.

Hemicyclaspis murchisoni (Egerton).

Portion of dorsal exoskeleton of cephalic shield from posterior end of inter-zonal part. Where the superficial layer is present, the pores of the mucous canal system are seen as small black dots; where it has been removed, the mucous canal system is visible. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8813.**—G. H. Piper Coll., 1898]. Approx. × 12 diam.

bl, basal layer; *iac*, inter-areal mucous canals, here represented by more or less closed grooves (at p_1, groove is completely closed); *ita*, intra-areal mucous canals (to be seen only where the superficial layer has been removed); *ml*, middle layer; p, pores of intra-areal mucous canals; p_1, pores of a closed inter-areal mucous canal; *sl*, superficial layer (easily recognizable by the presence of pores).

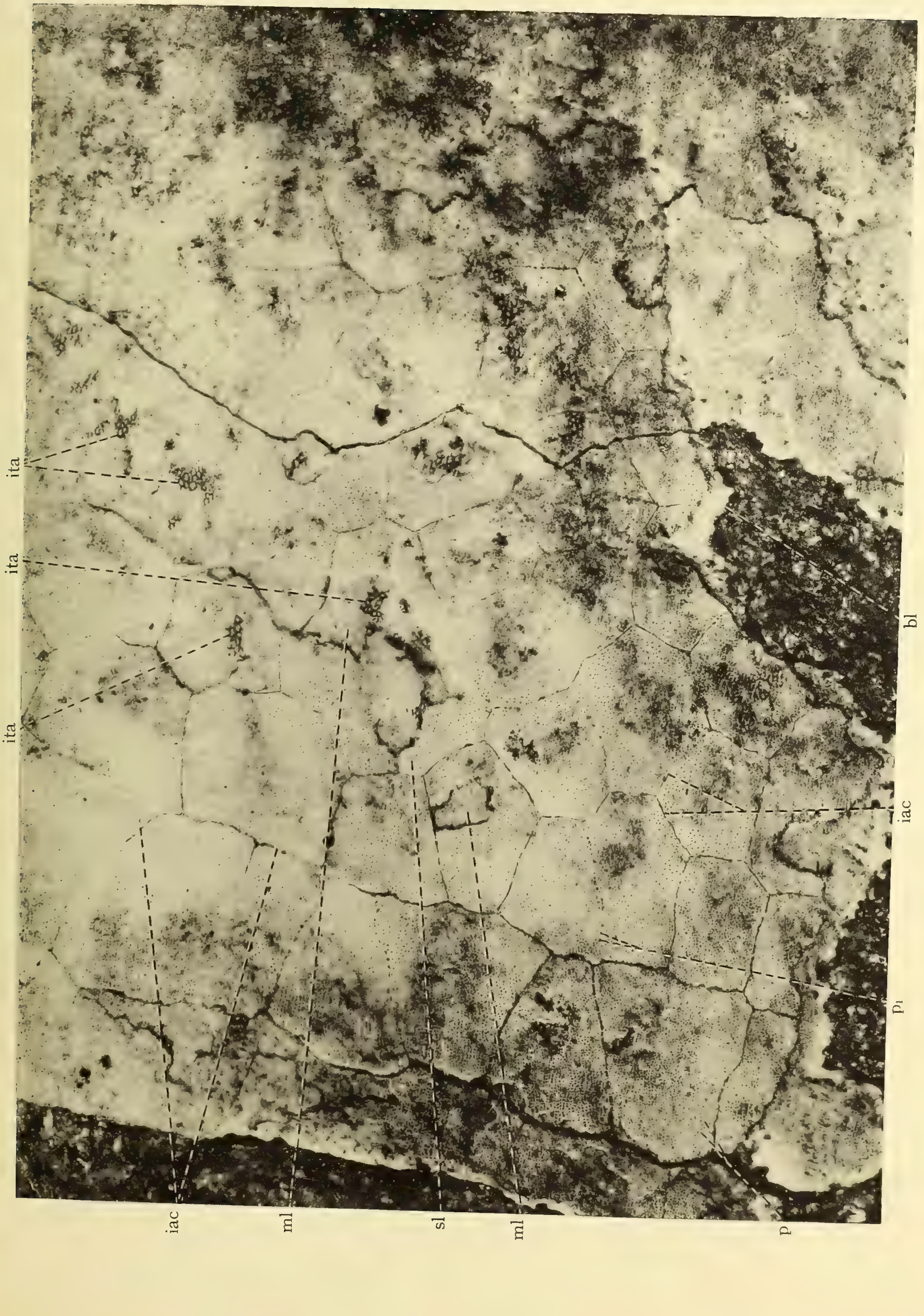

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PLATE 10.

Hemicyclaspis murchisoni (Egerton), var. *ludlowensis* nov.

FIG. 1.—Part of cephalic shield, inner view. The basal layer has been removed over a fairly large area to show the development of the mucous canal system. (See also Pl. 22, fig. 5.) Downtonian: Railway at Ludlow, Shropshire. HOLOTYPE. Museum of Practical Geology, London [no. **47807**.—R. Lightbody Coll.] Approx. × 10 diam.

Hemicyclaspis murchisoni (Egerton).

FIG. 2.—Inner surface of part of exoskeleton of cephalic shield prepared to show mucous canal system. The basal layer has been entirely, and the middle layer to a great extent, removed. (Same specimen as in Pl. 4, fig. 3, but further magnified.) Approx. × 25 diam.

Hemicyclaspis lightbodii (Lankester).

FIG. 3.—Rostral part of dorsal exoskeleton of cephalic shield. Downtonian: Ludlow, Shropshire. British Museum [no. **P. 16154**.—R. Lightbody Coll., *ex* Coll. Hereford Museum, 1932]. × 2 diam.

bl, basal layer; *c.asc*, superficial parts of ascending vascular canals; *ebc*, superficial external branches from radiating canals; *iac*, inter-areal canals or grooves; *ita*, intra-areal canals or grooves; *mc*, mucous canals in general; *ml*, middle layer; *rad.c*, radiating canals.

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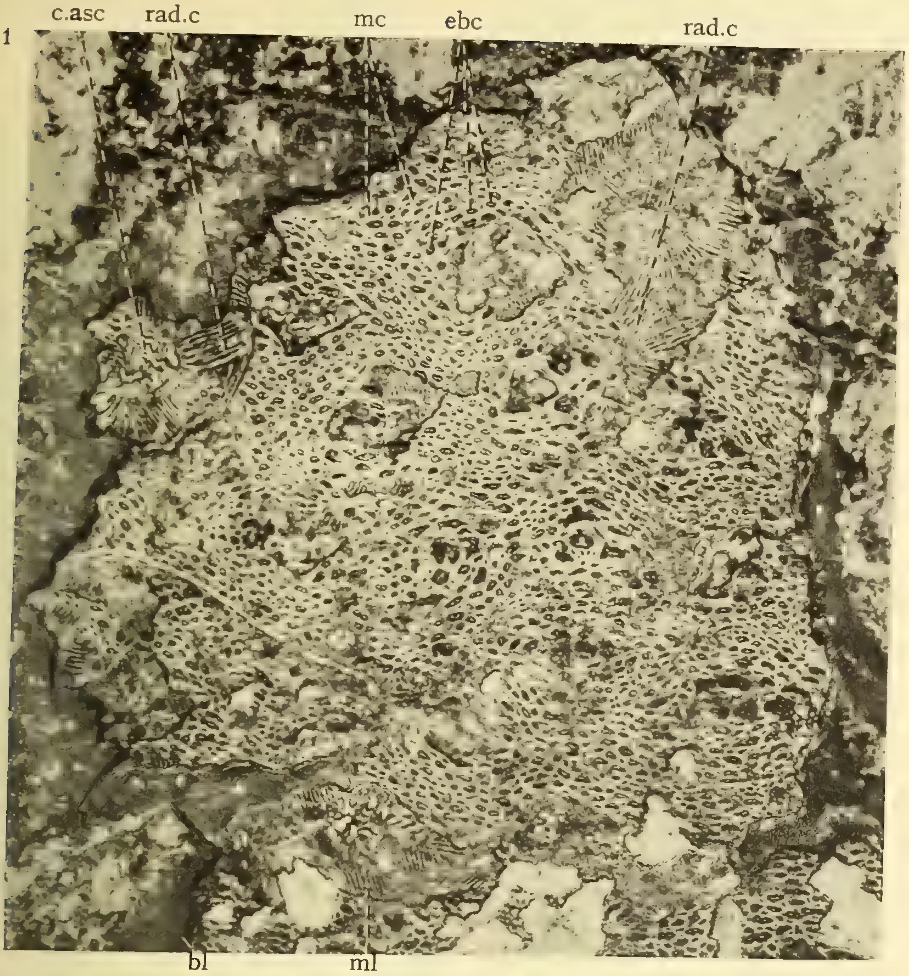

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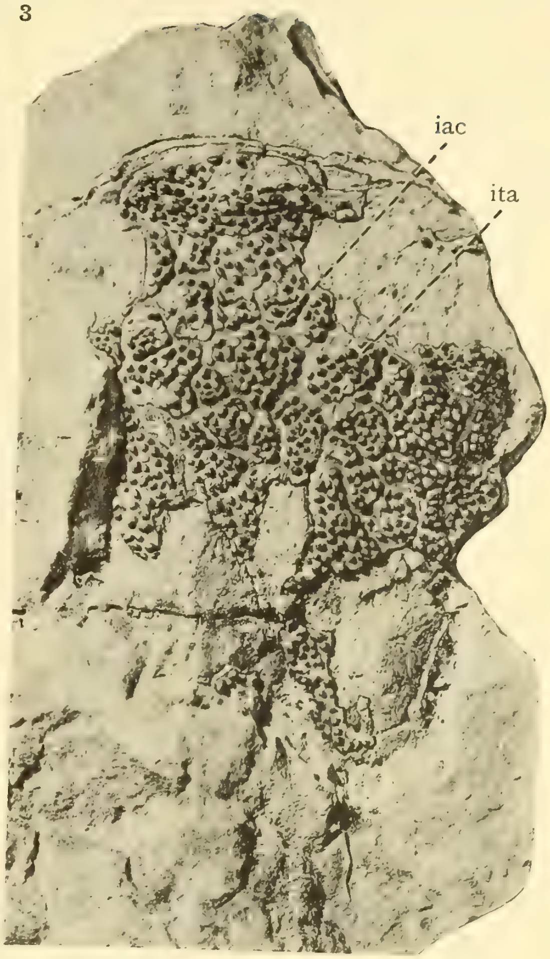

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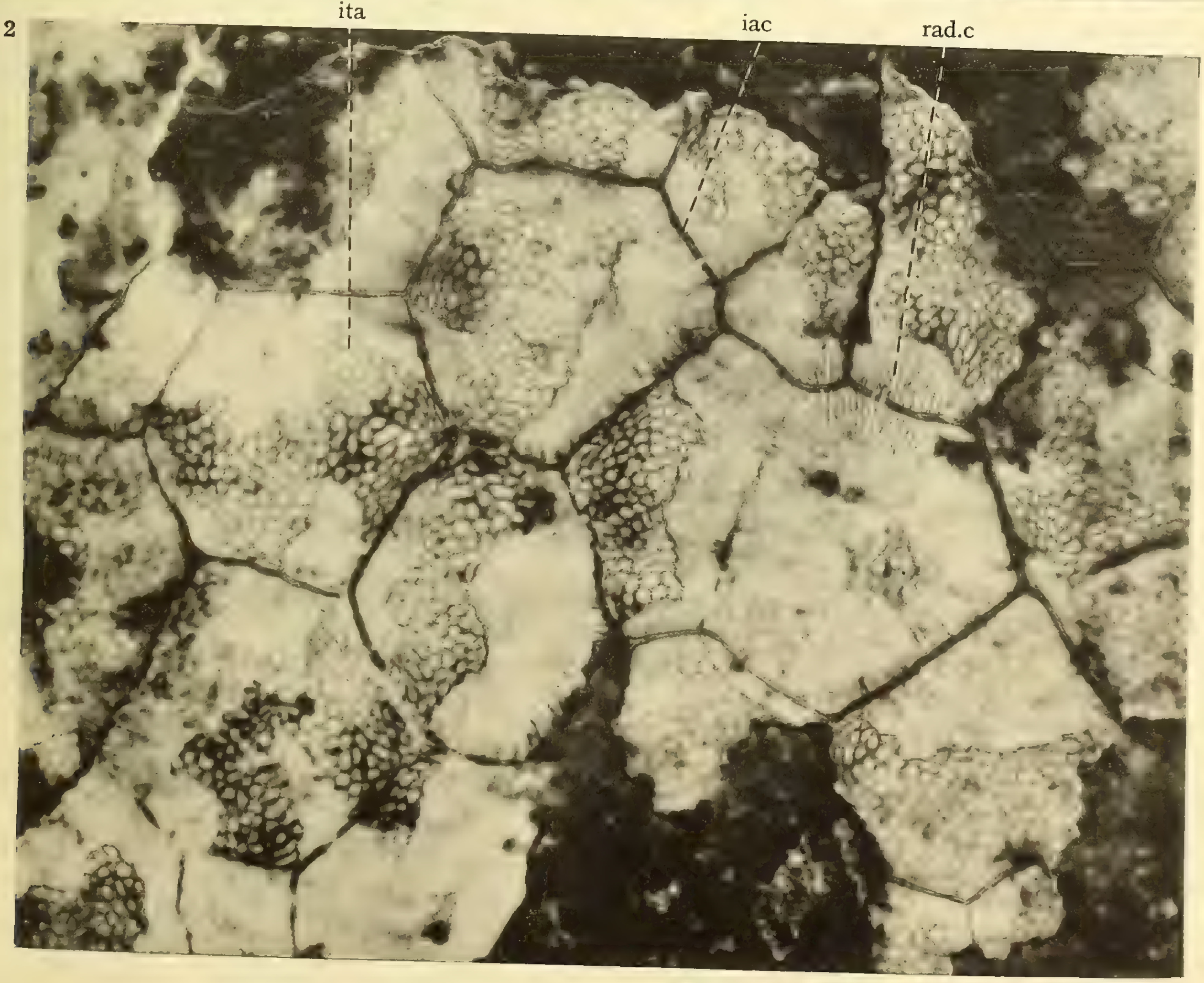

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PLATE 11.

Hemicyclaspis murchisoni (Egerton), (?) var. *ludlowensis* nov.

Fig. 1.—Imperfect cephalic shield, ventral view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8829.**—G. H. Piper Coll., 1898]. Nat. size.

Hemicyclaspis lightbodii (Lankester).

Fig. 2.—Imperfect cephalic shield, dorsal view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8828.**—G. H. Piper Coll., 1898]. Nat. size.

Cephalaspis salweyi Egerton.

Fig. 3.—Posterior dorsal part of cephalic shield with dorsal spine, from right side. (See also Pl. 36, figs. 1, 2.) Lower Old Red Sandstone: Heightington, Worcestershire. British Museum [nos. **P. 188** and **P. 190** (counterparts).—Weaver Jones Coll., 1880]. Nat. size.

Fig. 4.—Cephalic shield, dorsal view. Lower Old Red Sandstone: Cradley, Herefordshire. British Museum [no. **41186.**—Purchased 1868]. Nat. size.

d.sp, dorsal spine; *k*, branchial fossae (ventral ends); *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *obr.f*, oralo-branchial fenestra; *orb*, orbital opening; *pin*, pineal opening; *ps*, pectoral sinus; *r.sin*, venous ring-sinuses immediately underlying exoskeleton (impressions of their grooves on basal surface of exoskeleton).

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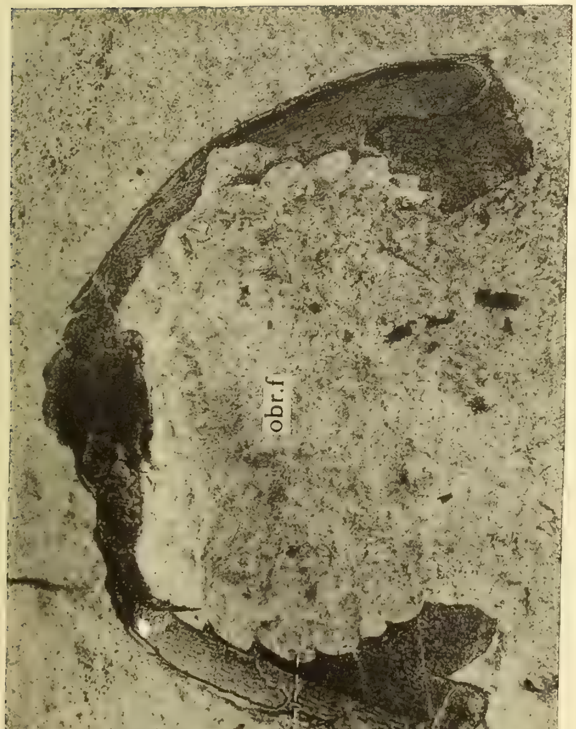

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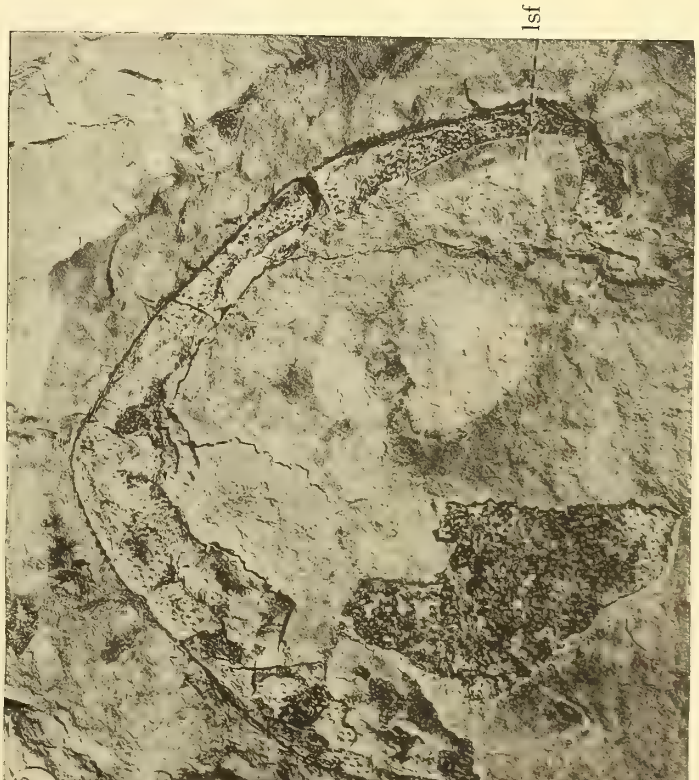

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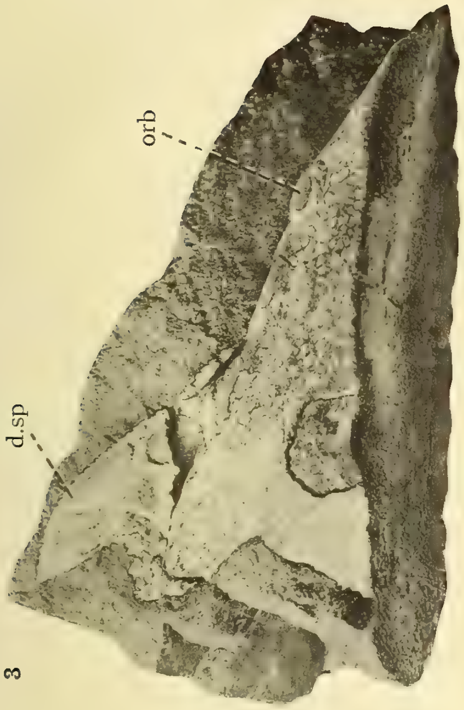

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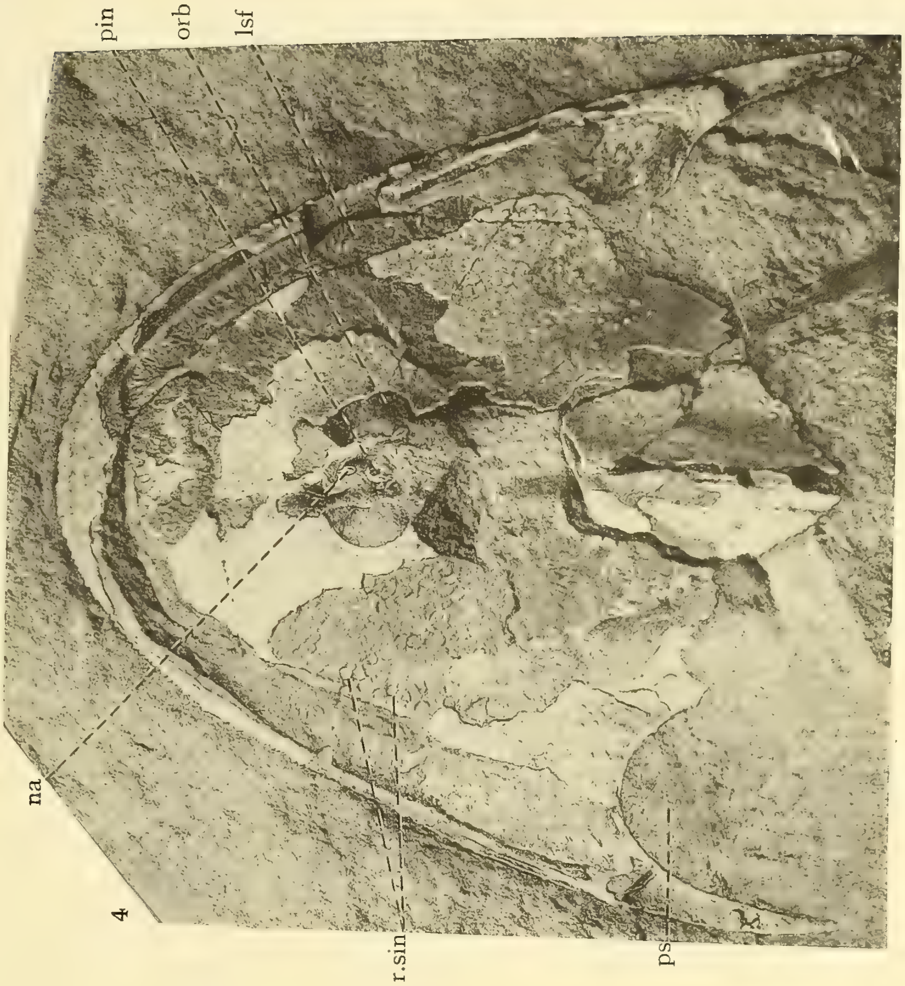

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PLATE 12.

Cephalaspis salweyi Egerton.

FIG. 1.—Cephalic shield, dorsal view. (See also Pl. 58, fig. 3.) Lower Old Red Sandstone: Cradley, Herefordshire. British Museum [no. **42132.**—T. Baugh Coll., 1870]. Nat. size.

FIG. 2.—Somewhat distorted cephalic shield, dorsal view. (See also Pl. 66, fig. 1.) Lower Old Red Sandstone: Heightington, Worcestershire. British Museum [no. **P. 191.**—Weaver Jones Coll., 1880]. Nat. size.

FIG. 3.—Fragment of cornu. Lower Old Red Sandstone: Skirrid Fawr, near Abergavenny, Monmouthshire. British Museum [no. **P. 5033.**—J. E. Lee Coll., 1885]. Nat. size.

FIG. 4.—Detached cornu. Lower Old Red Sandstone: Skirrid Fawr, near Abergavenny, Monmouthshire. British Museum [no. **P. 5033***a*.—J. E. Lee Coll., 1885]. Nat. size.

dsf, dorsal electric field; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *pin*, pineal opening; *ps*, pectoral sinus; *r.sin*, venous ring-sinuses immediately underlying exoskeleton (impressions of their grooves on basal surface of exoskeleton).

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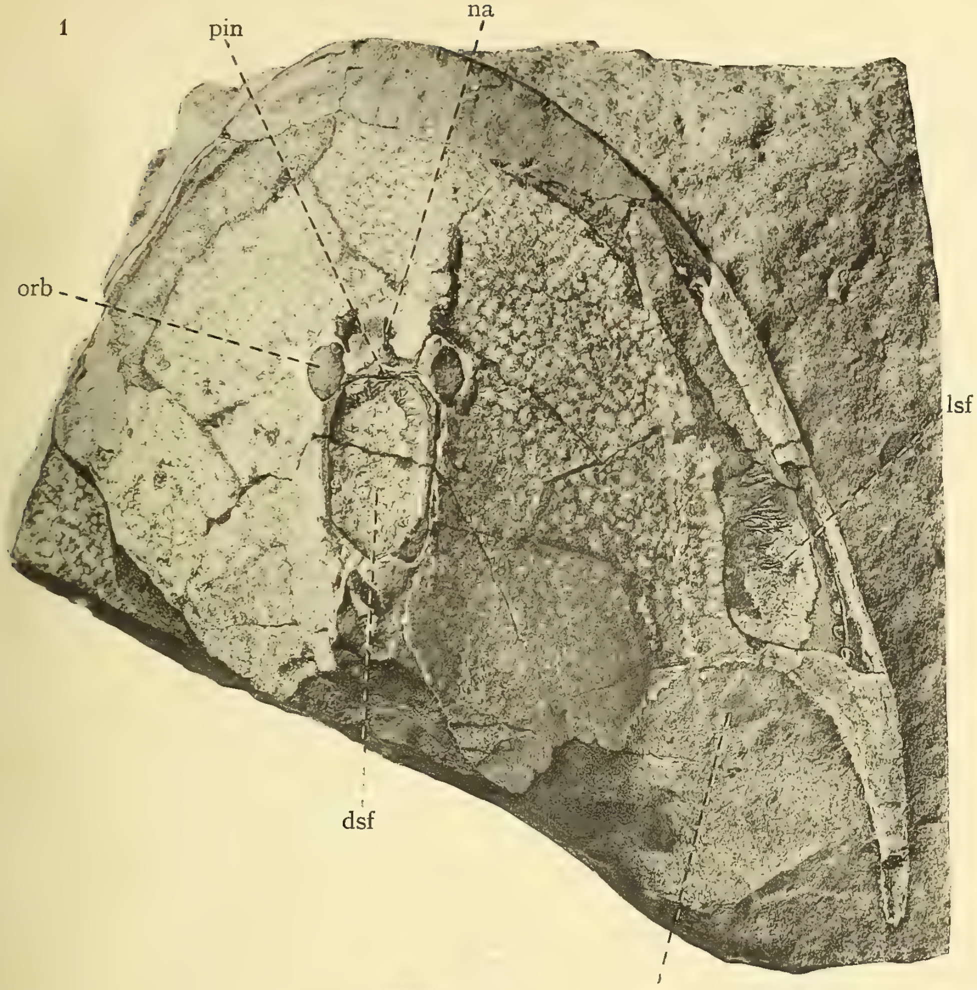

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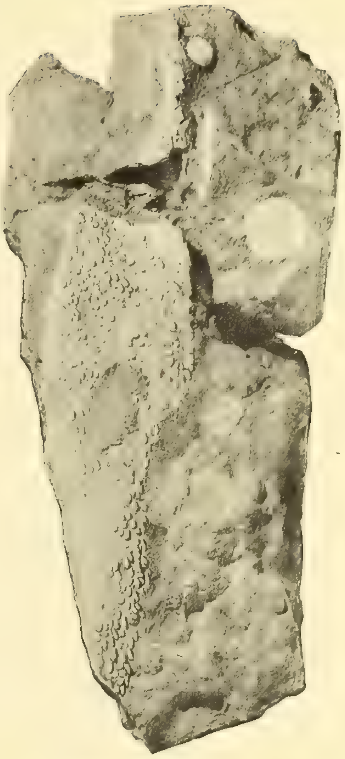

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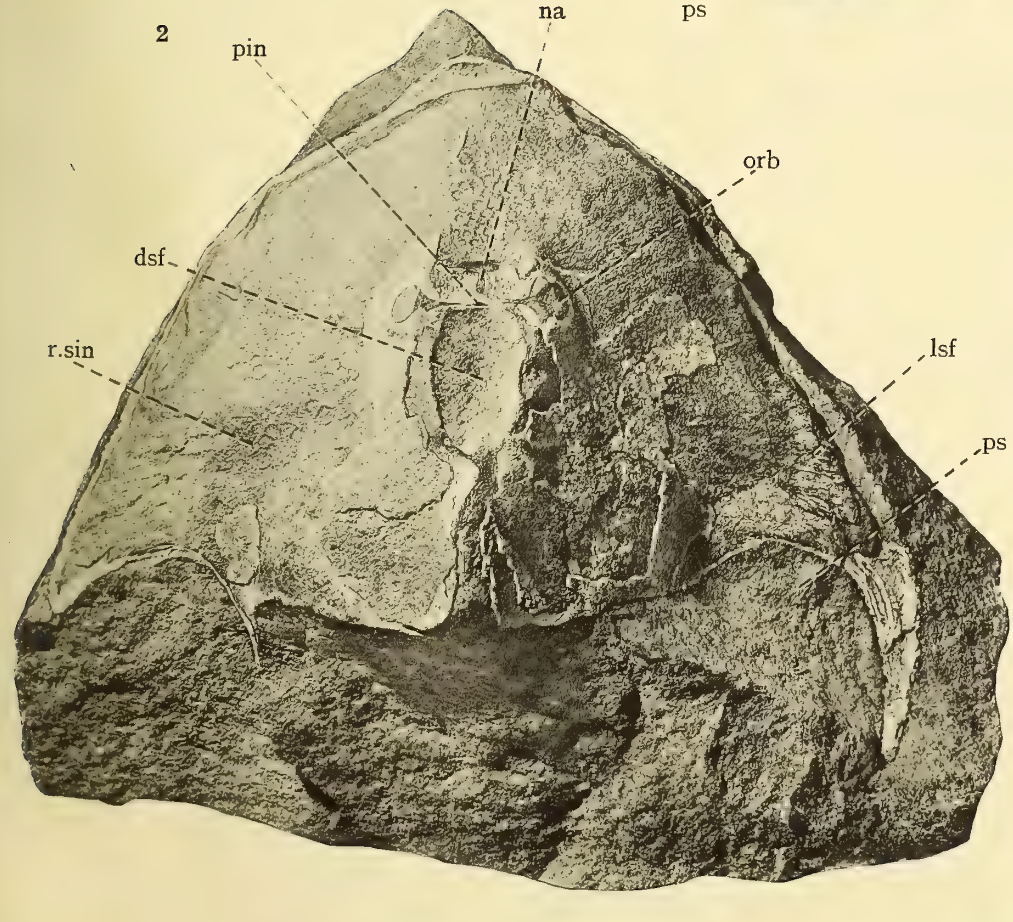

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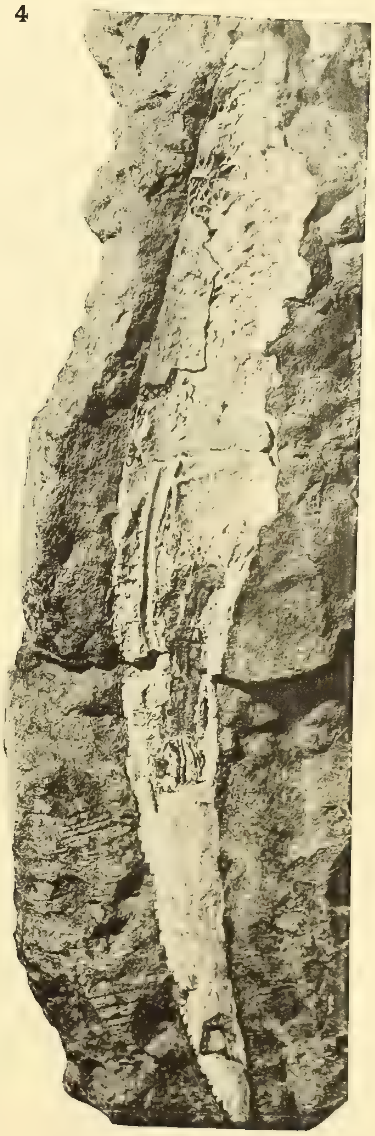

CEPHALASPIS

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PLATE 13.

Cephalaspis salweyi Egerton.

FIG. 1.—Cephalic shield wanting cornua and adjacent parts, ventral view. The ornamentation is mostly destroyed. Lower Old Red Sandstone: Skirrid Fawr, near Abergavenny, Monmouthshire. British Museum [no. **P. 5032.**—J. E. Lee Coll., 1885]. Nat. size.

FIG. 2.—Same specimen, dorsal view. Nat. size.

d_1, canal for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf*, dorsal electric field; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *obr.f*, oralo-branchial fenestra; *orb*, orbital opening; *pd*, pineal depression; pin_1, pineal opening at bottom of pineal depression; *ps*, pectoral sinus.

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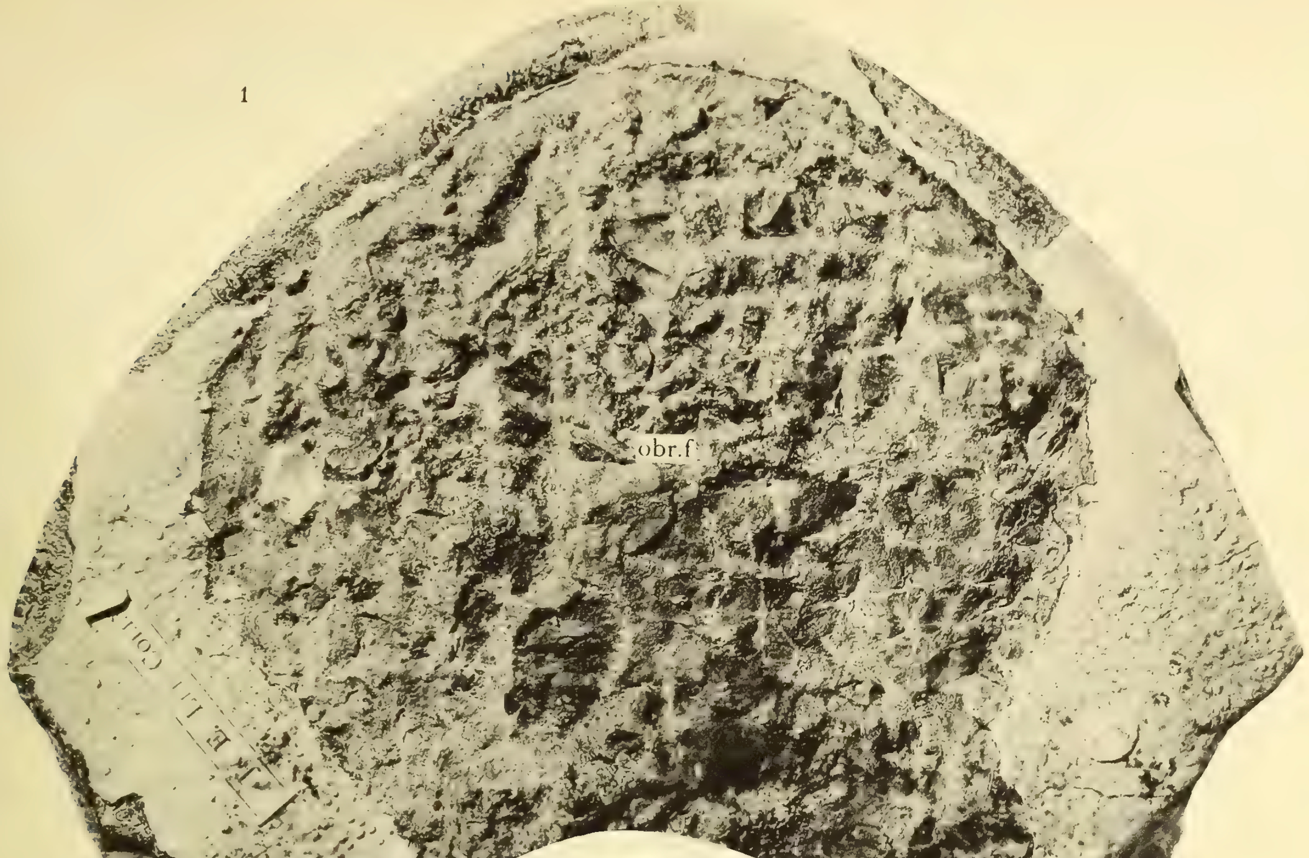

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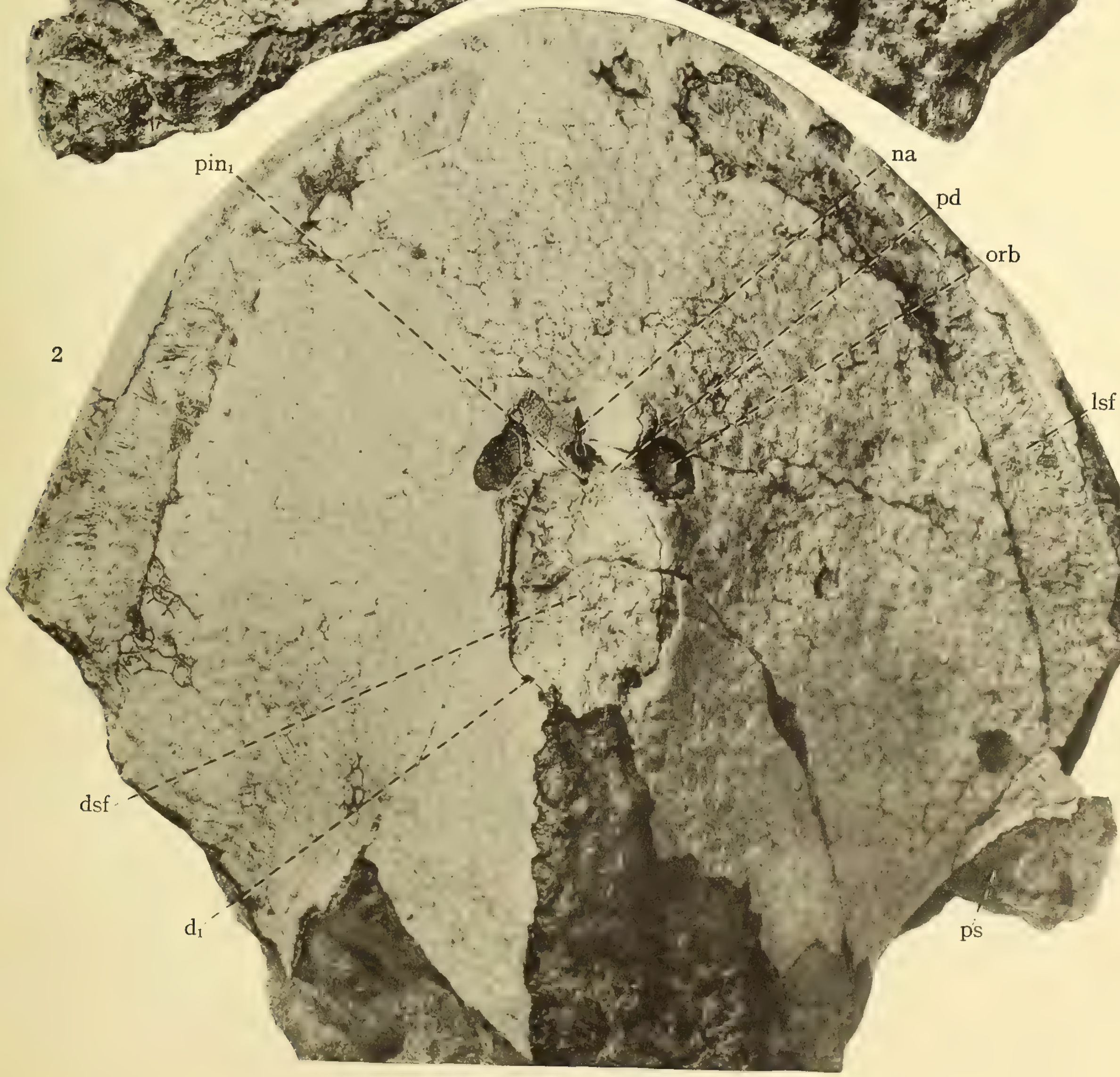

CEPHALASPIS

BRITISH MUSEUM
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PLATE 14.

Cephalaspis langi, sp. nov.

FIG. 1.—Distorted cephalic shield doubtfully referred to this species, dorsal view. The exoskeleton is present only here and there, and is represented by the basal layer only. Lower Old Red Sandstone: Cradley, Herefordshire. British Museum [no. **46878.**—Purchased, 1875]. × 2 diam.

FIG. 2.—Cephalic shield and anterior part of scale-covered division of trunk, dorsal view. The exoskeleton of the dorsal side is represented mainly by an internal cast. On the right side parts of the oralo-branchial chamber are to be seen. Lower Old Red Sandstone: near Pontrilas,* Herefordshire. HOLOTYPE. Ludlow Museum [no. **E/a/20.I**]. × 2 diam.

FIG. 3.—Right side of cephalic shield and anterior part of squamation preserved largely in impression. Lower Old Red Sandstone: near Pontrilas,* Herefordshire. Ludlow Museum [no. **E/a/20.II**]. × 2 diam.

FIG. 4.—Anterior part of squamation of left side of same specimen, preserved almost entirely in impression. × 2 diam.

Cephalaspis heightingtonensis, sp. nov.

FIG. 5.—Cephalic shield showing exoskeleton of dorsal side of shield and parts of endoskeleton, ventral view. Lower Old Red Sandstone: Heightington, Worcestershire. HOLOTYPE. British Museum [no. **38033.**—Purchased, 1864]. × 2 diam.

FIG. 6.—Counterpart of same specimen, dorsal view. × 2 diam.

FIG. 7.—Cephalic shield, dorsal view. The exoskeleton is largely destroyed, and anteriorly the supraoral field and the aortic ridge are exposed. Lower Old Red Sandstone: Heightington, Worcestershire. British Museum [no. **42142.**—T. Baugh Coll., 1870]. × 2 diam.

dls, dorso-lateral scales; *dpr*, supra-oral field; *dsf*, dorsal electric field; *d.sp*, dorsal spine; *ibs*, interbranchial septa; *k*, branchial fossa; *ls*, lateral scales; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; *r.aort*, aortic ridge; sel_1–sel_6, canals of nerves of lateral electric field; $v.ls_1$, supposed canal of dorso-lateral superficial vein 1; *vrs*, ventro-lateral scales; V_1, canal of n. profundus.

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* See p. 200.

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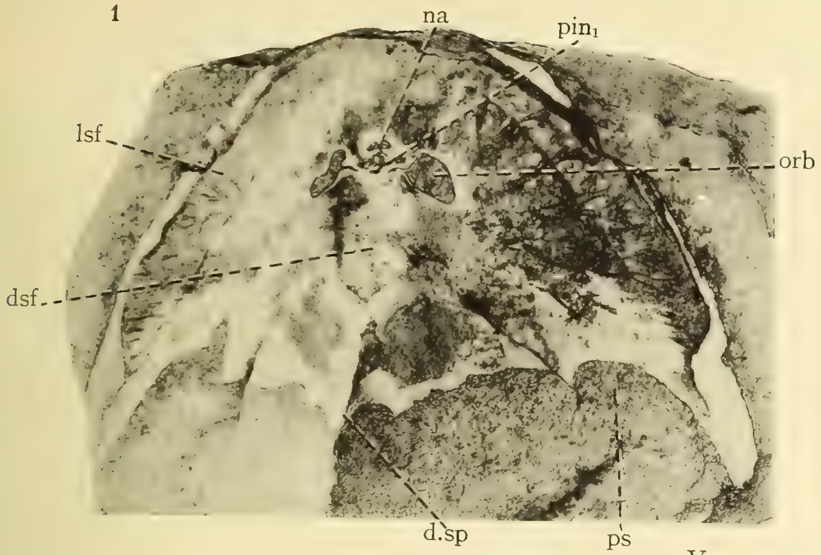

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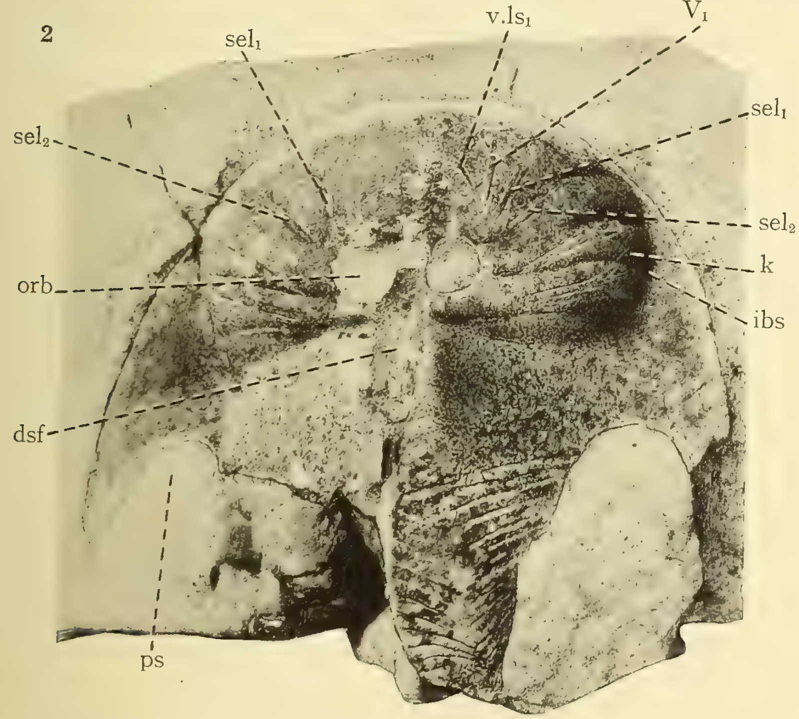

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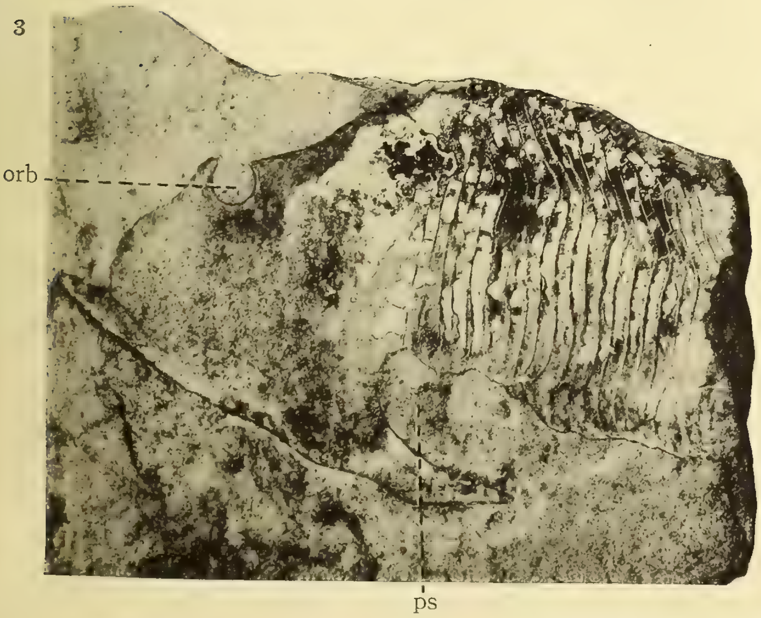

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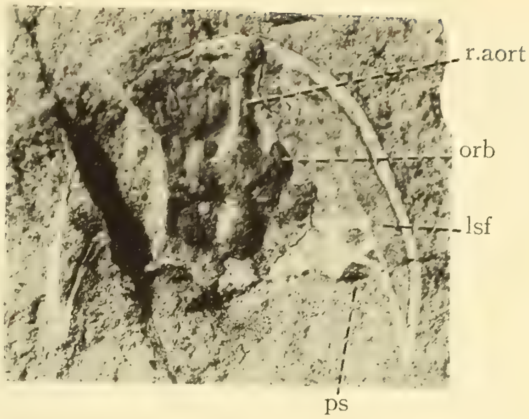

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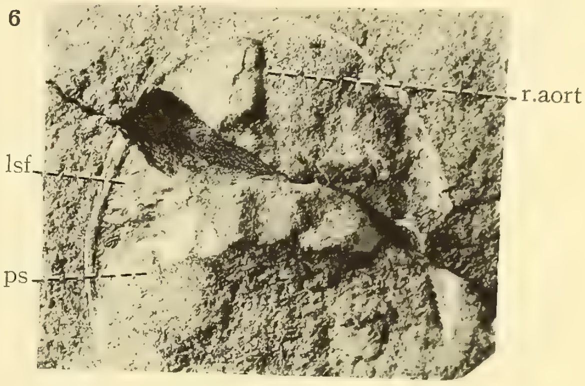

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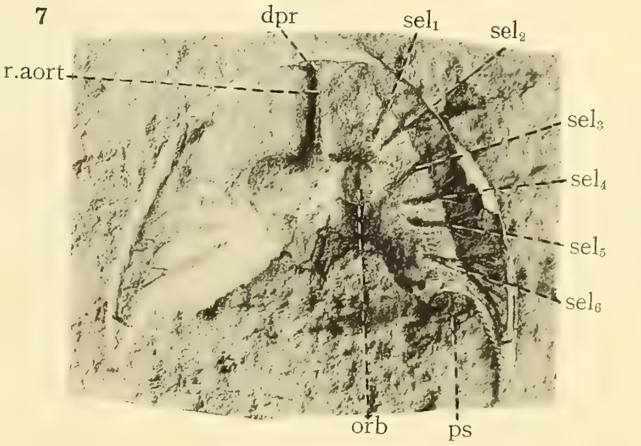

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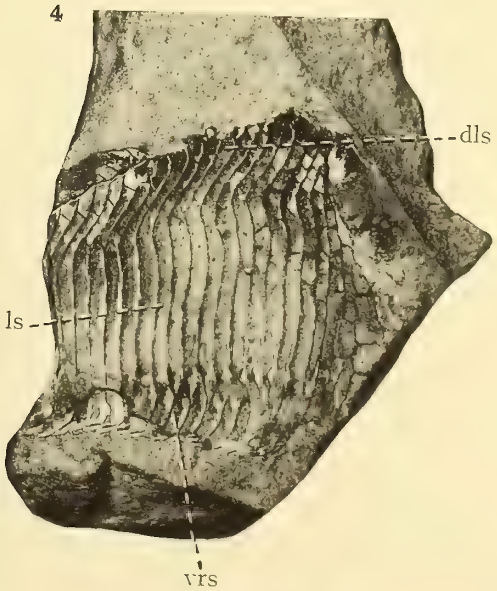

CEPHALASPIS

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PLATE 15.

Cephalaspis lyelli Agassiz.

Fig. 1.—Cephalic shield doubtfully referred to this species, dorsal view. The dorsal exoskeleton of the shield has been almost entirely weathered away. Lower Old Red Sandstone: Brechin, Forfarshire. British Museum [no. **P. 6945***a*.—Hugh Mitchell Coll., 1893]. Nat. size.

Cephalaspis fletti, sp. nov.

Fig. 2.—Cephalic shield, dorsal view. The dorsal exoskeleton of the shield is represented only by its basal layer. Lower Old Red Sandstone: Leverhill, near Leominster, Herefordshire. Museum of Practical Geology, London [no. **47809.**—J. F. Crouch Coll.]. × 1½ diam.

Fig. 3.—Cephalic shield, dorsal view. The dorsal exoskeleton of the shield is either represented by the basal layer only or entirely absent. (See also Pl. 22, fig. 2.) Lower Old Red Sandstone: Downton Hall, near Ludlow, Shropshire. Holotype. Ludlow Museum [no. **1.**—A. Marston Coll.]. × 1½ diam.

Fig. 4.—Imperfect impression of cephalic shield doubtfully referred to this species, dorsal view. Lower Old Red Sandstone: loc. unknown. Museum of Practical Geology, London [no. **G.S. 6474.**—R. I. Murchison Coll.]. × 1½ diam.

Cephalaspis whitbachensis, sp. nov.

Fig. 5.—Cephalic shield, dorsal view. The dorsal exoskeleton of the shield is represented only by the most basal part of the basal layer. Lower Old Red Sandstone: Whitbach, near Ludlow, Shropshire. Holotype. Ludlow Museum [no. **7.**—A. Marston Coll.]. × 1½ diam.

Cephalaspis cradleyensis, sp. nov.

Fig. 6.—Distorted but fairly complete cephalic shield, dorsal view. The dorsal exoskeleton of the shield is represented by the basal layer only. Lower Old Red Sandstone: Cradley, Herefordshire. Holotype. British Museum [no. **P. 5375.**—H. B. Holl Coll., 1887]. × 2 diam.

d_1, canal for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf*, dorsal electric field; *d.sp*, impression of dorsal spine; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *pd*, pineal depression; *pin*, pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; sel_1–sel_5, canals of nerves 1–5 of lateral electric field.

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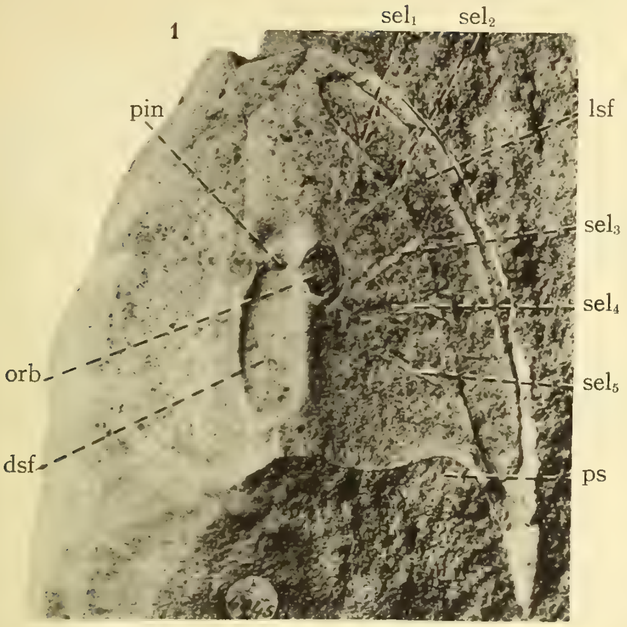

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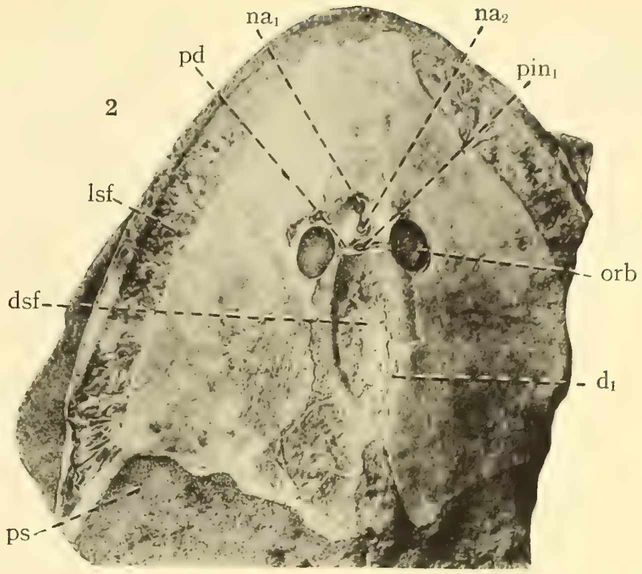

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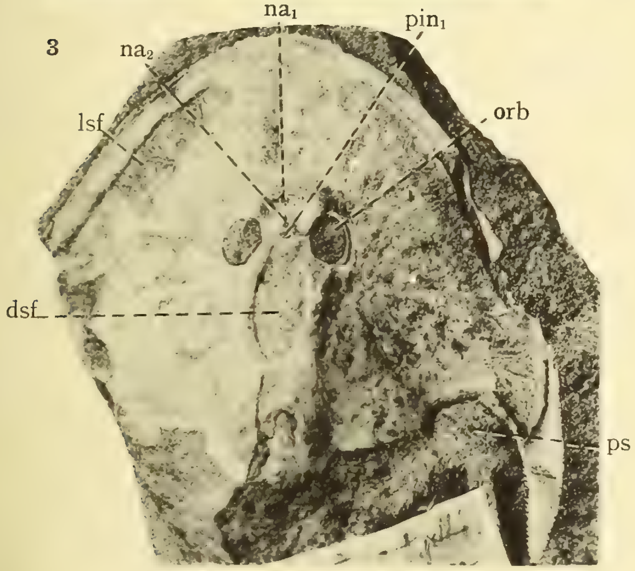

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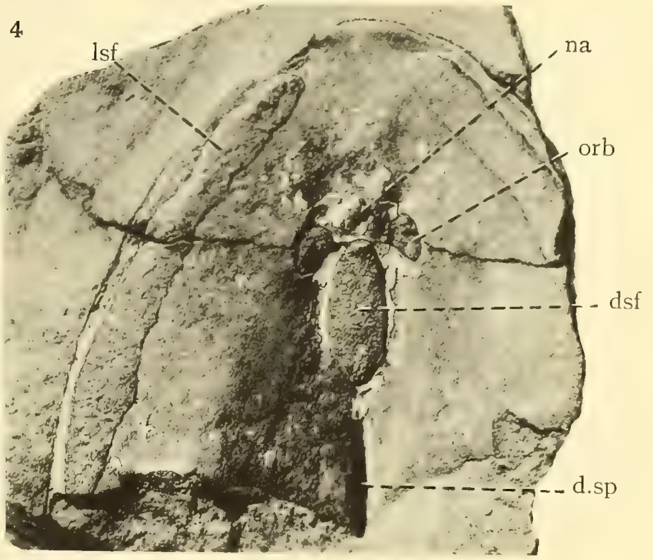

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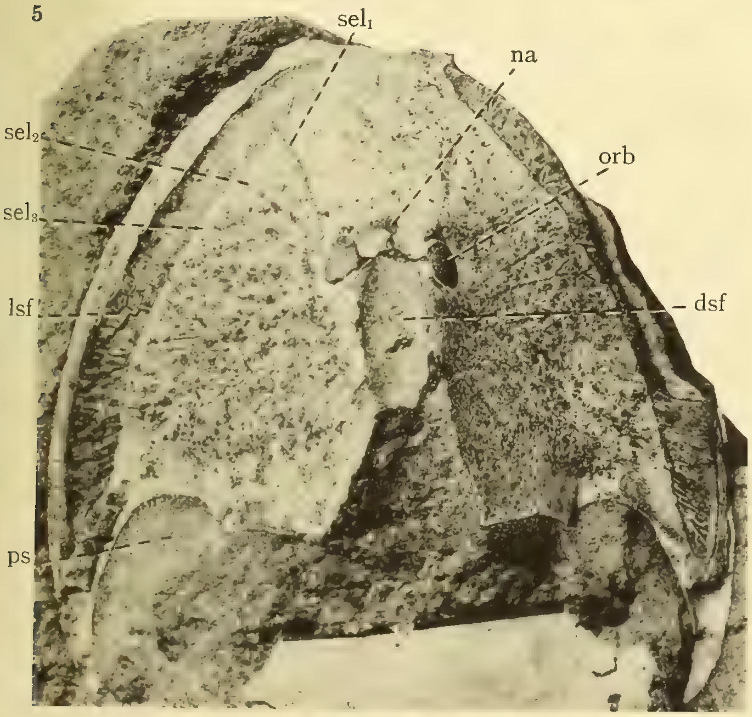

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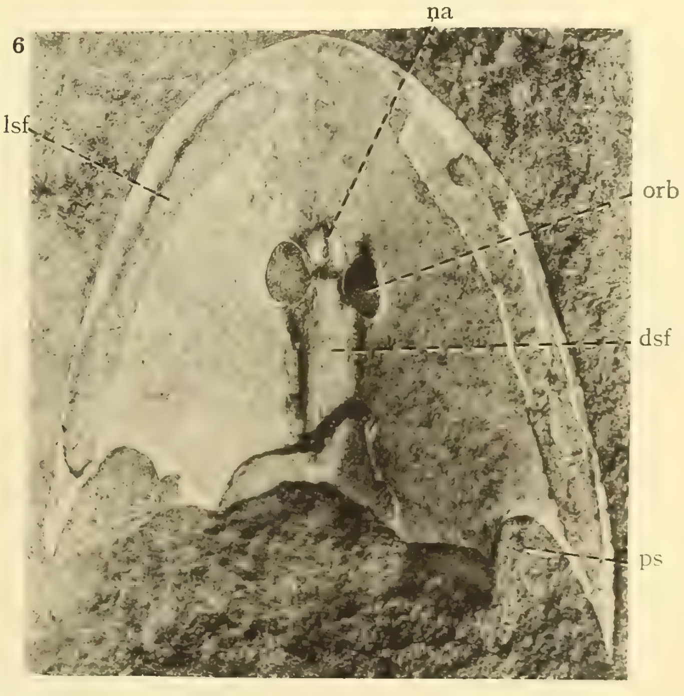

CEPHALASPIS

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PLATE 16.

Hemicyclaspis murchisoni (Egerton).

Fig. 1.—Part of scale-covered division of trunk seen from left side. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 16153.**—G. H. Piper Coll., *ex* Coll. Hereford Museum, 1932]. Slightly magnified.

Cephalaspis fletti, sp. nov.

Fig. 2.—Cephalic shield doubtfully referred to this species, dorsal view. Lower Old Red Sandstone: Leverhill, near Leominster, Herefordshire. Museum of Practical Geology, London [no. **47811.**—J. F. Crouch Coll.]. × > 1½ diam.

Cephalaspis agassizi Lankester.

Fig. 3.—Somewhat distorted cephalic shield, dorsal view. The dorsal exoskeleton of the shield is imperfectly preserved. Lower Old Red Sandstone: Cradley, Herefordshire. Lectotype. University Museum, Oxford [not numbered.—R. B. Grindrod Coll., 1882]. × 2 diam.

Fig. 4.—Cephalic shield, dorsal view. The dorsal exoskeleton of the shield is largely destroyed. Lower Old Red Sandstone: Whitbach, near Ludlow, Shropshire. Museum of Practical Geology, London [no. **47815**]. × 1½ diam.

C, caudal fin; D_2, dorsal fin; *dsf*, dorsal electric field; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *pd*, pineal depression; pin_1, pineal opening on dorsal side of endocranial component of cephalic shield; *ps*, pectoral sinus; sel_1–sel_3, sel_6, canals for nerves 1–3 and 6 of lateral electric field; $v.ls_1$, $v.ls_2$, canals of dorso-lateral superficial veins 1 and 2.

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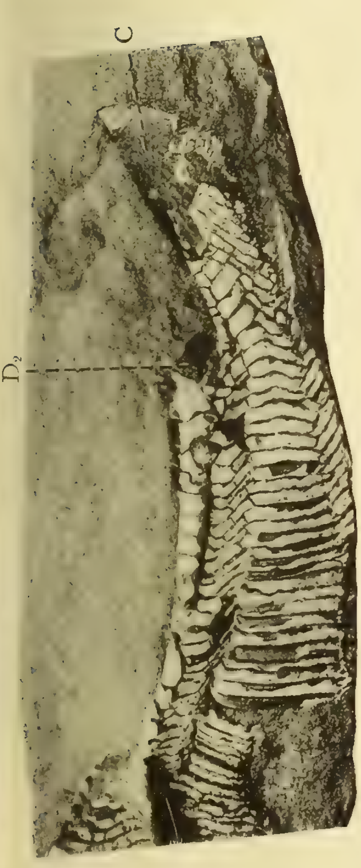

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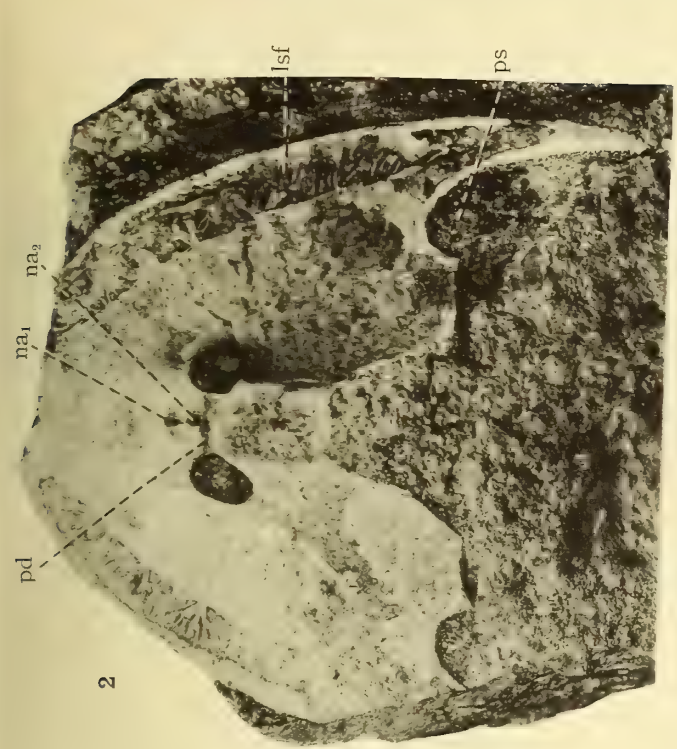

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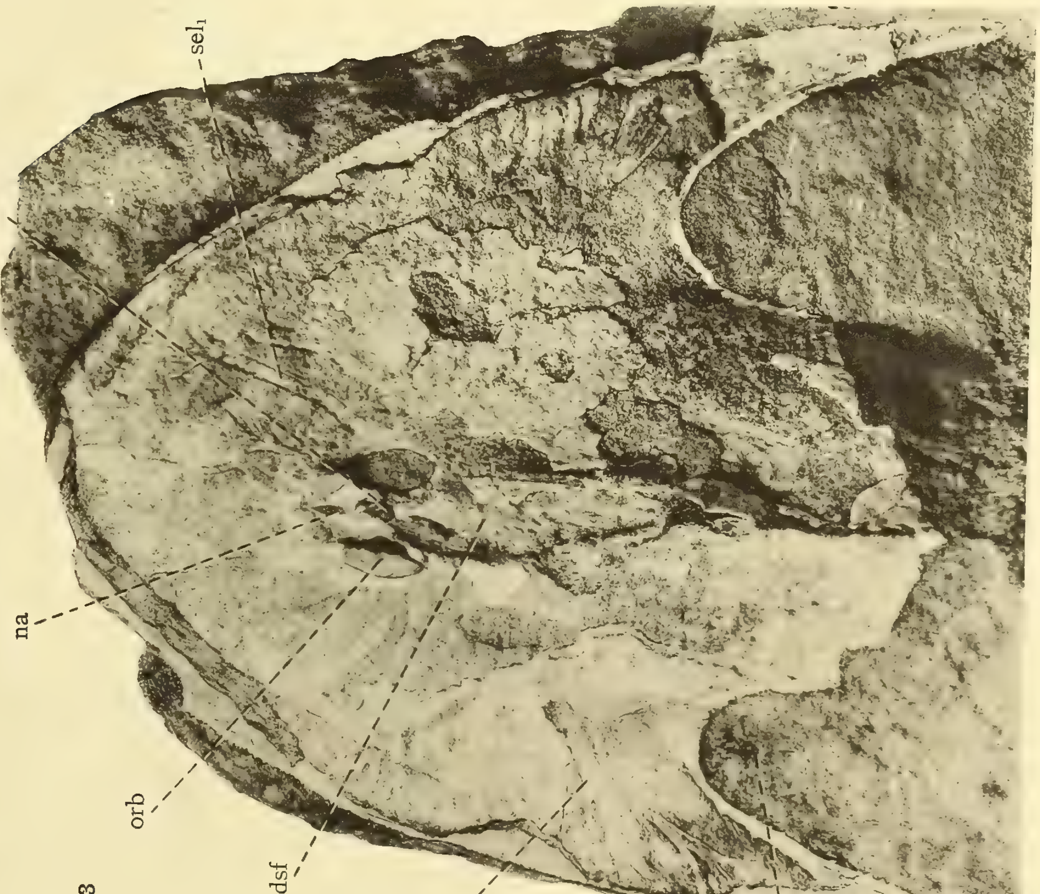

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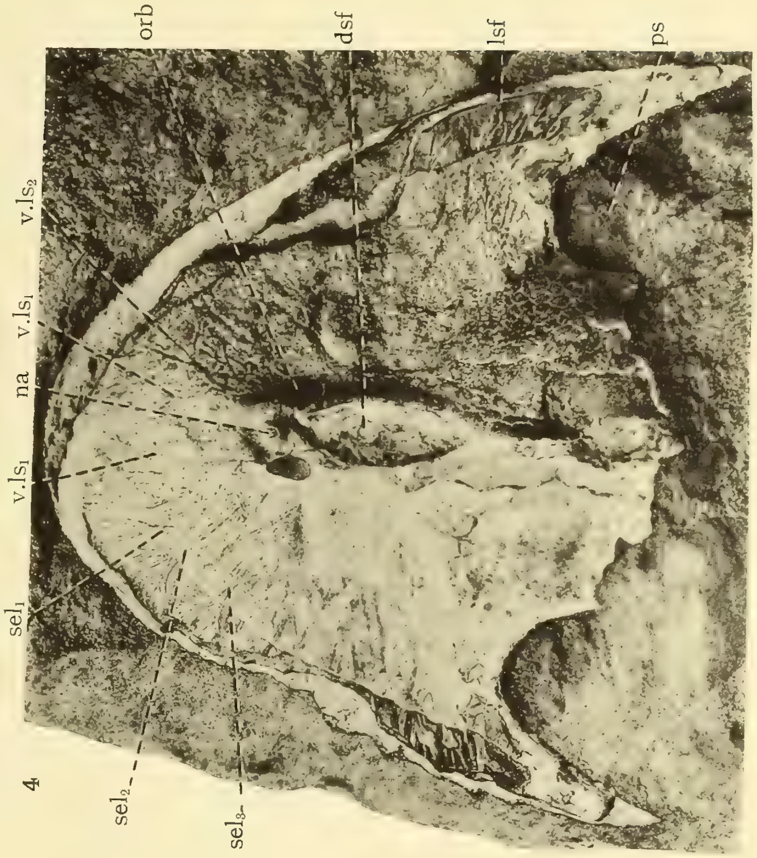

HEMICYCLASPIS and CEPHALASPIS

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PLATE 17.

Cephalaspis websteri, sp. nov.

FIG. 1.—Impression of dorsal surface of cephalic shield. Lower Old Red Sandstone: loc. uncertain. HOLOTYPE. British Museum [no. **P. 16150.**—*ex* Coll. Dundee Museum, 1932]. Nat. size.

Cephalaspis lankesteri, sp. nov.

FIG. 2.—Cephalic shield, dorsal view. Only the basal layer of the dorsal exoskeleton is preserved. Lower Old Red Sandstone: Whitbach, near Ludlow, Shropshire. HOLOTYPE. British Museum [no. **45943.**—R. Lightbody Bequest, 1874]. × 1½ diam.

FIG. 3.—Counterpart of right side of same specimen. The right cornu is well preserved, and the exoskeletal remains consist principally of the superficial layer and the superficial parts of the middle layer. (See also Pl. 56, fig. 2.) British Museum [no. **P. 16155.**—*ex* Coll. Hereford Museum, 1932]. × 3 diam.

cm, groove possibly corresponding to pre-opercular or jugal sensory canal of fishes; *cmm*, groove possibly corresponding to middle head-line of pit-organs of fishes; $cmm_1 + cmm_2 + cmm_3$, grooves corresponding either to posterior head-line of pit-organs, or to supra-temporal cross-commissure, of fishes; *dsf*, dorsal electric field; *d.sp*, dorsal spine (in fig. 1, impression only); *ifc*, infra-orbital groove; *lc*, cephalic division of main lateral line; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *pin*, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; sel_1–sel_2, canals of 1st and 2nd nerves of lateral electric field.

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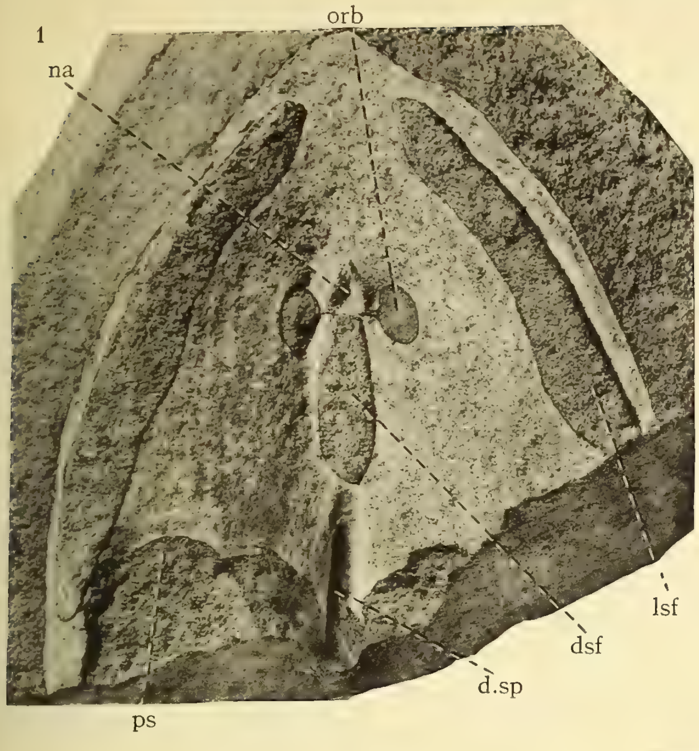

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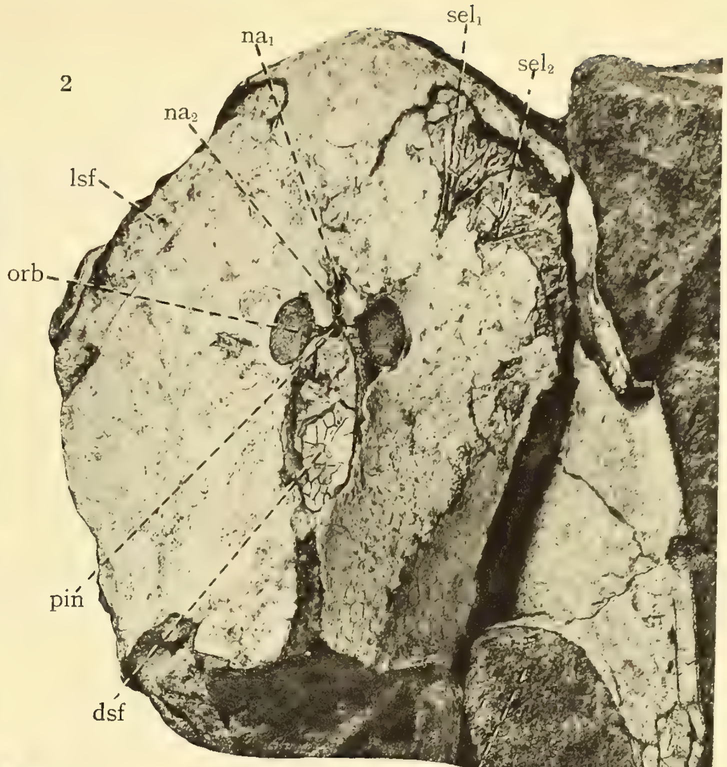

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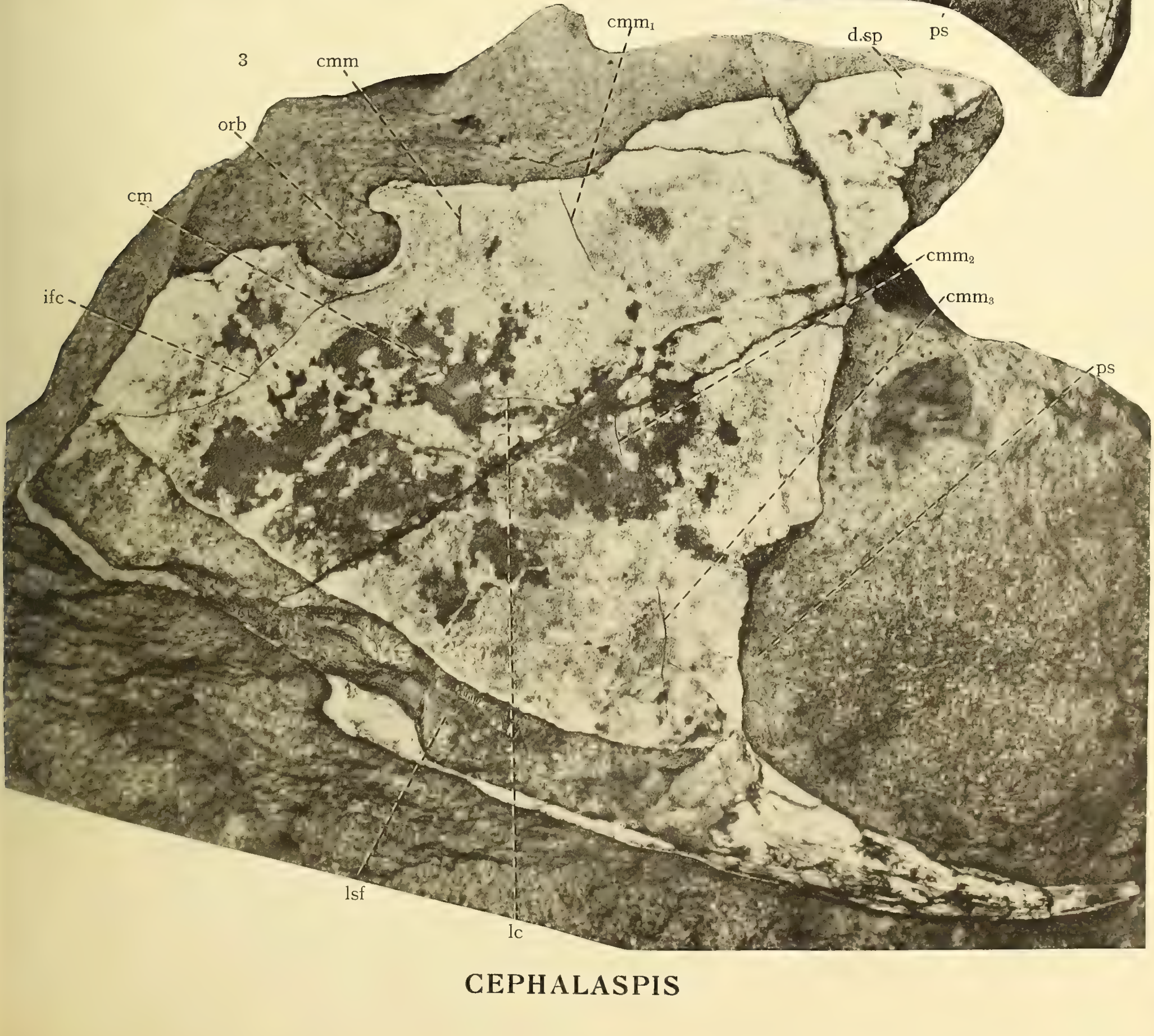

CEPHALASPIS

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PLATE 18.

Cephalaspis sp. nov. ?

Fig. 1.—Cephalic shield, dorsal view. Lower Old Red Sandstone: Whitbach, near Ludlow, Shropshire. British Museum [no. **45946.**—R. Lightbody Bequest, 1874]. Nat. size.

Cephalaspis fletti, sp. nov.

Fig. 2.—Cephalic shield doubtfully referred to this species, dorsal view. The dorsal exoskeleton of the shield is imperfectly preserved. (See also Pl. 22, fig. 1.) Lower Old Red Sandstone: Downton Hall, near Ludlow, Shropshire. Ludlow Museum [no. **6.**—A. Marston Coll.]. × 2 diam.

Cephalaspis whitei, sp. nov.

Fig. 3.—Cephalic shield, dorsal view. The exoskeleton is imperfectly preserved. (Pls. 61 and 62 are from enlarged photographs of the sub-aponeurotic (sub-cutaneous) vascular plexus, etc. of this specimen.) Lower Old Red Sandstone: loc. unknown. British Museum [no. **P. 16156.**—*ex* Coll. Hereford Museum, 1932]. Nat. size.

Fig. 4.—Dorsal exoskeleton of cephalic shield, inner view. Lower Old Red Sandstone: Whyle Rock, near Leominster, Herefordshire. Museum of Practical Geology, London [no. **G.S. 6471.**—R. I. Murchison Coll.]. Nat. size.

Fig. 5.—Cephalic shield, dorsal view. The exoskeleton of the dorsal side is wanting except in a few places. Lower Old Red Sandstone: Whitbach, near Ludlow, Shropshire. Museum of Practical Geology, London [no. **G.S. 6443**]. × 1½ diam.

Fig. 6.—Cephalic shield doubtfully referred to this species, dorsal view. The dorsal exoskeleton of the shield is for the most part wanting, so that several of the main vascular canals of the sub-aponeurotic (sub-cutaneous) vascular plexus and some of the nerve-canals are exposed. Lower Old Red Sandstone: Heightington, Worcestershire. British Museum [no. **P. 192.**—Weaver Jones Coll., 1880]. × 1½ diam.

a.iol, lateral infra-orbital branch of canal of a. facialis; $a.sm_1$, $a.sm_2$, canals of dorso-lateral superficial arteries 2 and 3; *dsf*, dorsal electric field; *dpr*, supra-oral field; *d.sp*, dorsal spine; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *pd*, pineal depression; *pin*, pin_1, pineal opening on dorsal surface of endoskeleton of cephalic shield; *ps*, pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field; $v.ls_1$–$v.ls_6$, canals of dorso-lateral superficial veins 1–6; V_1, canal of n. profundus.

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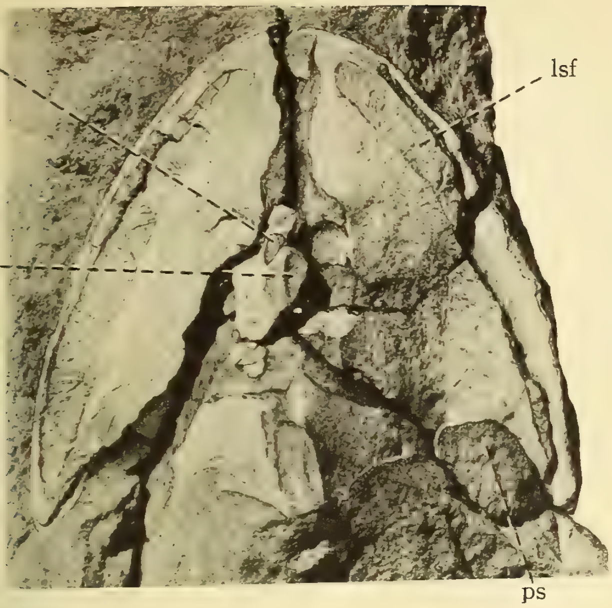

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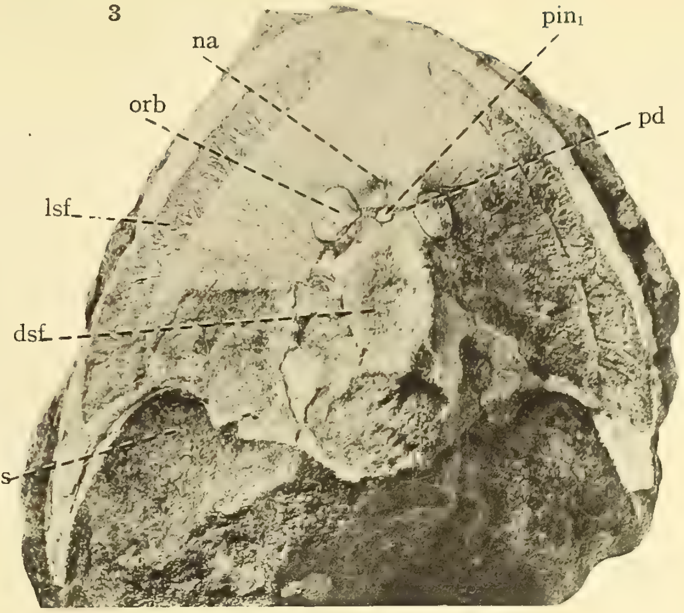

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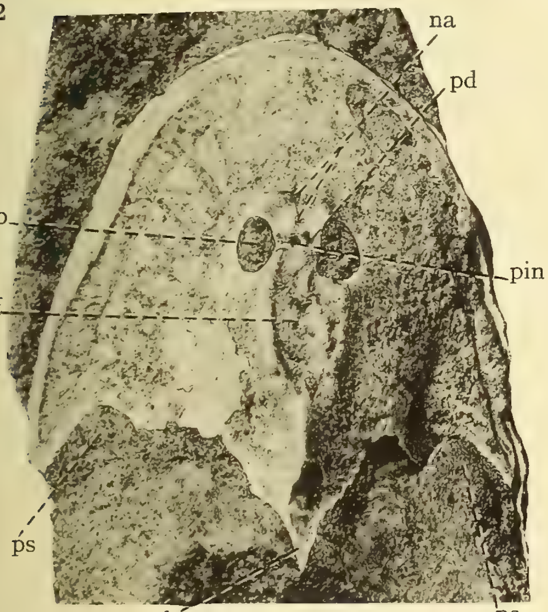

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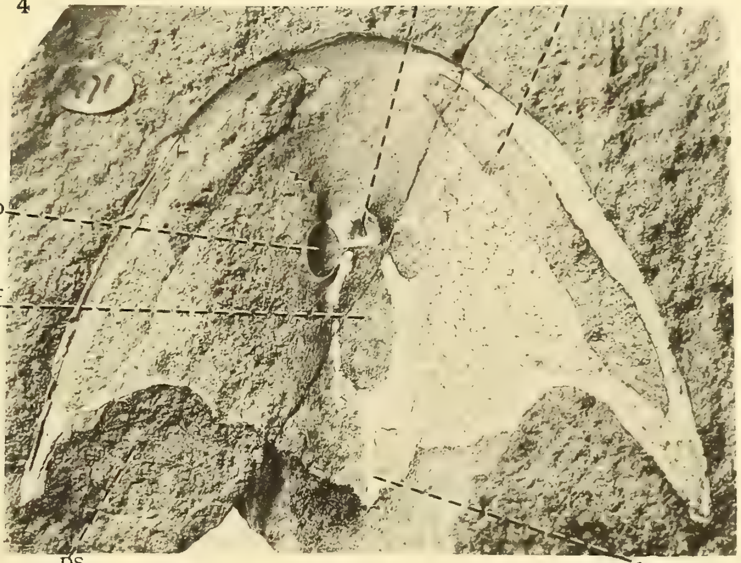

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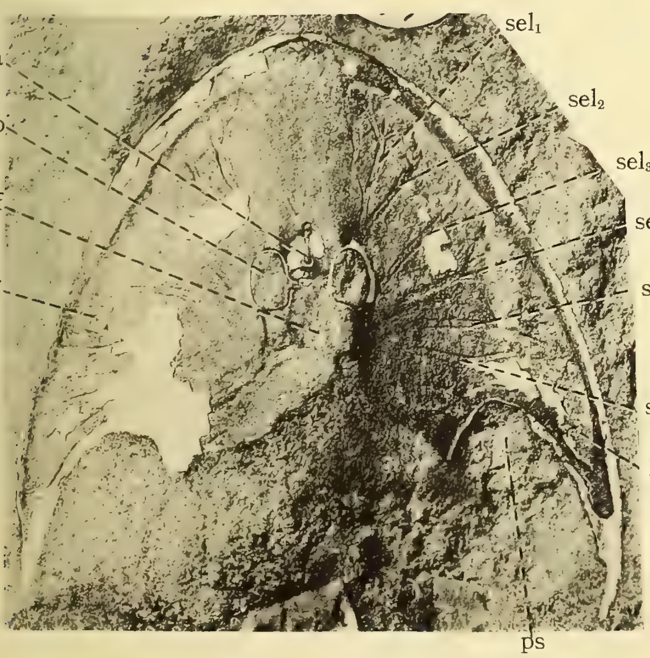

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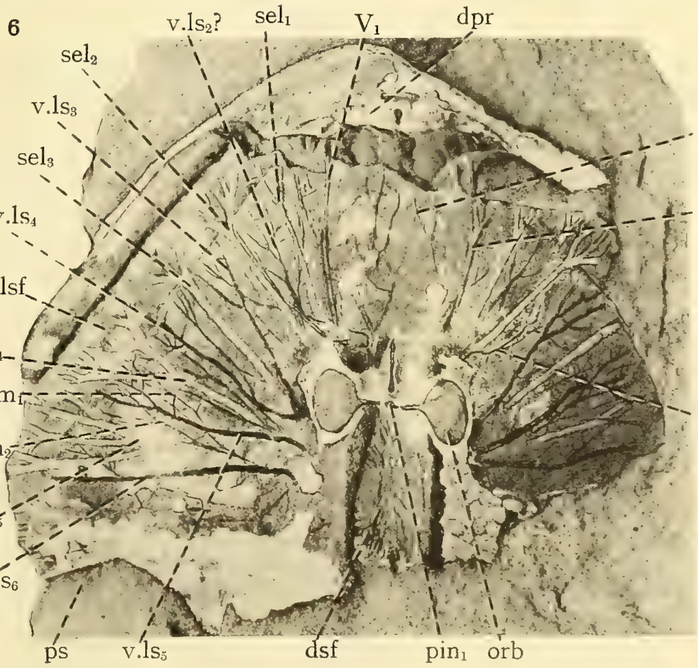

CEPHALASPIS

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PLATE 19.

Cephalaspis whitei, sp. nov.

FIG. 1.—Cephalic shield, dorsal view. The exoskeleton is preserved in places only. Lower Old Red Sandstone: loc. unknown. Museum of Practical Geology, London [no. **47808.**—R. Lightbody Coll.]. × 1½ diam.

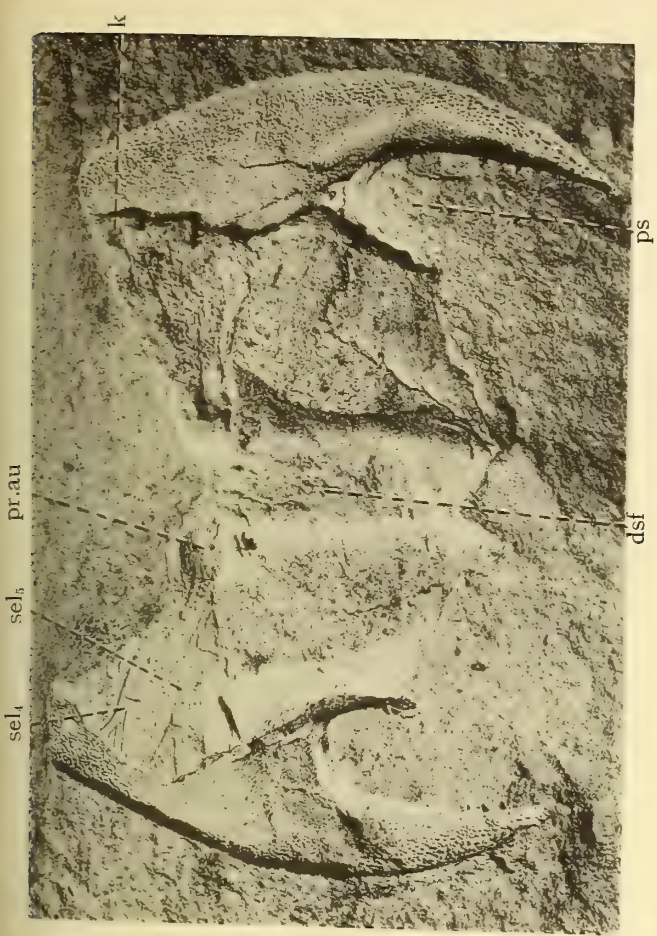
FIG. 2.—Cephalic shield, dorsal view. The exoskeleton is almost entirely wanting. Lower Old Red Sandstone: Downton Hall, near Ludlow, Shropshire. Ludlow Museum [no. **2.**—A. Marston Coll.]. × 1½ diam.

Cephalaspis watsoni, sp. nov.

FIG. 3.—Posterior half of cephalic shield, dorsal view. The exoskeleton is preserved as an impression only. Lower Old Red Sandstone: Rossie Priory, Perthshire. Museum of Practical Geology, London [no. **47788.**—Kinnaird Coll.]. × 1½ diam.

FIG. 4.—Impression of dorsal surface of cephalic shield. Lower Old Red Sandstone: Rossie Priory, Perthshire. HOLOTYPE. Museum of Practical Geology, London [no. **47786.**—Kinnaird Coll.]. × 1½ diam.

a.iol, lateral infra-orbital branch of canal of a. facialis; $a.sm_1$–$a.sm_2$, *a.sp*, canals of dorso-lateral superficial arteries 2–4; *dsf*, dorsal electric field; *d.sp*, impression of dorsal spine; *ifc*, infra-orbital sensory canal groove; *k*, branchial fossa; *lsf*, lateral electric field; *na*, naso-hypophysial opening; na_1, anterior division of naso-hypophysial aperture (opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *p.a*, pectoral angle of cornu; *pd*, pineal depression; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *pr.au*, impression of vestibular division of labyrinth cavity; *ps*, pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field; $v.ls_3$–$v.ls_6$, canals of dorso-lateral superficial veins 3–6; V_1, canal of n. profundus.



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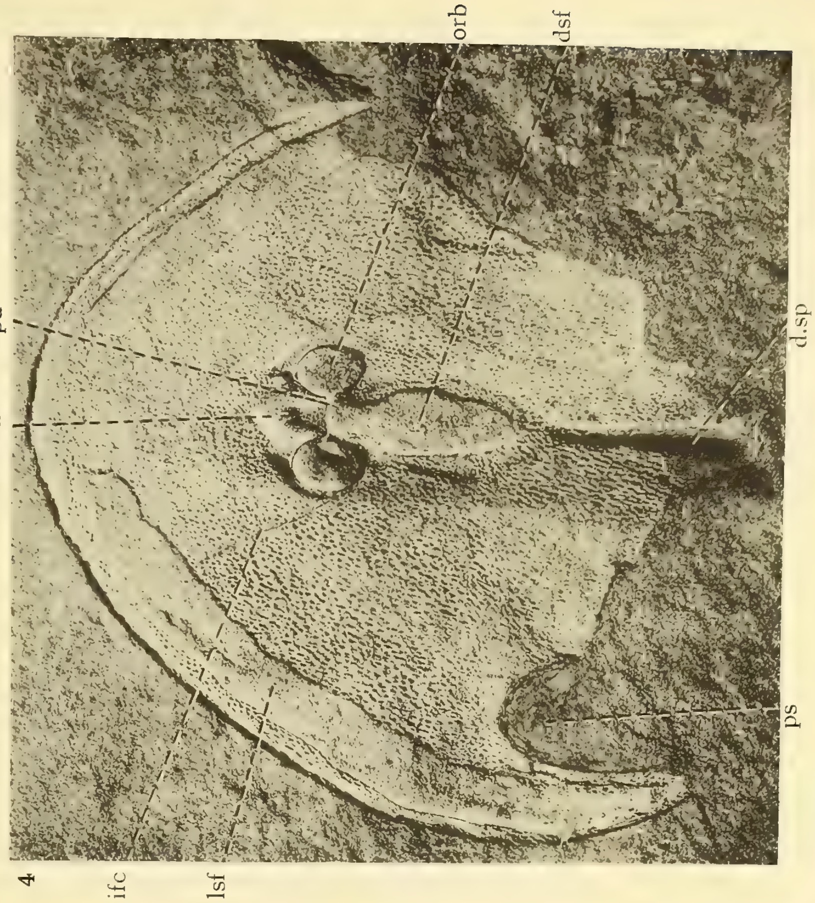

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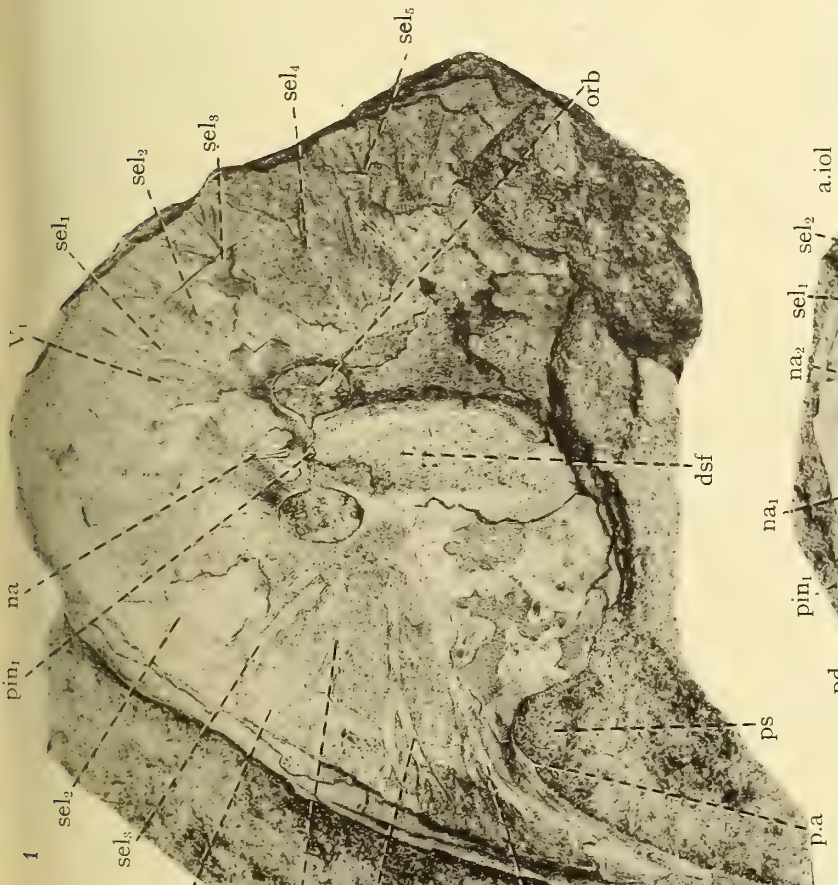

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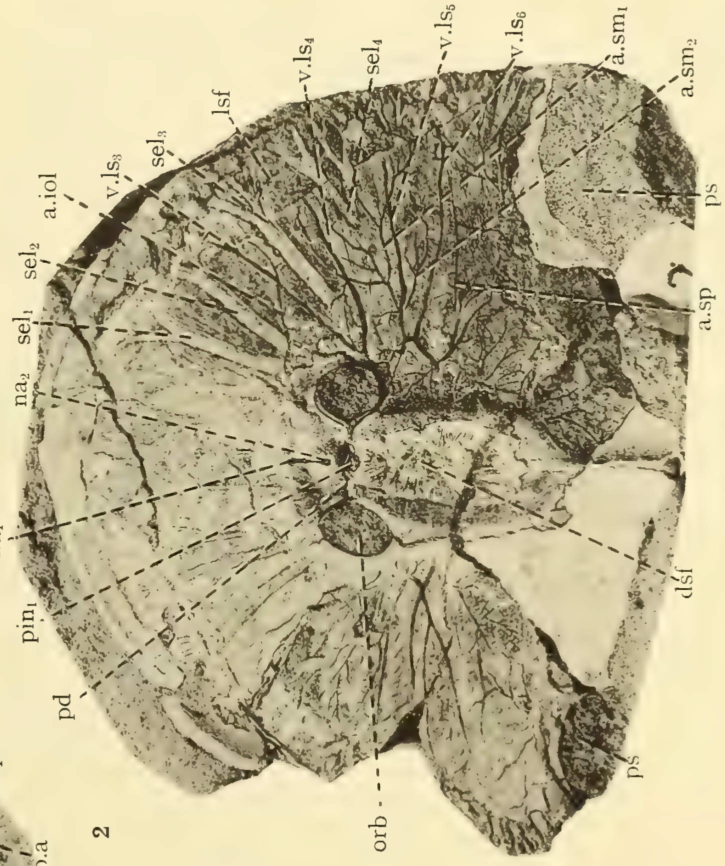

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CEPHALASPIS

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PLATE 20.

Cephalaspis woodwardi, sp. nov.

FIG. 1.—Dorsal exoskeleton of cephalic shield, internal view. Lower Old Red Sandstone: Asylum Grounds, Abergavenny, Monmouthshire. HOLOTYPE. Museum of Practical Geology, London [no. **47789.**—D. M. McCullough Coll.]. × 1½ diam.

FIG. 2.—Left half of dorsal exoskeleton of cephalic shield, internal view. Lower Old Red Sandstone: Asylum Grounds, Abergavenny, Monmouthshire. Museum of Practical Geology, London [no. **47791.**—D. M. McCullough Coll.]. × 1½ diam.

Cepalaspis whitei, sp. nov.

FIG. 3.—Cephalic shield, dorsal view. The exoskeleton of the left side is almost entirely destroyed, so that the canals of the sub-aponeurotic (sub-cutaneous) vascular plexus are well exposed. Rostrally the cast of part of the oralo-branchial chamber is shown. (See also text-fig. 9; Pl. 21; Pl. 32, fig. 6.) Lower Old Red Sandstone: Downton Hall, near Ludlow, Shropshire. HOLOTYPE. British Museum [no. **P. 5048.**—J. E. Lee Coll., 1885]. × 2 diam.

dpr, impression of supra-oral field; *dsf,* dorsal electric field; *ifc,* infra-orbital sensory canal groove; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb,* orbital opening; *p.a,* pectoral angle of cornu; *pin,* pineal opening; *ps,* pectoral sinus; *r.aort,* impression of aortic ridge; sel_1–sel_6, canals of nerves of lateral electric field; V_1, canal of n. profundus.

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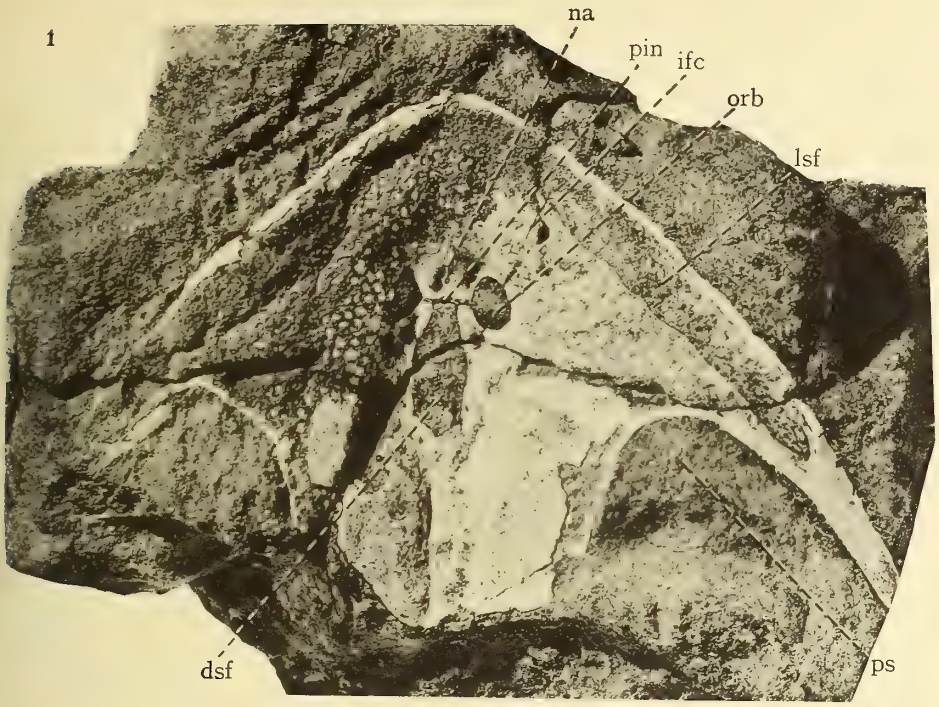

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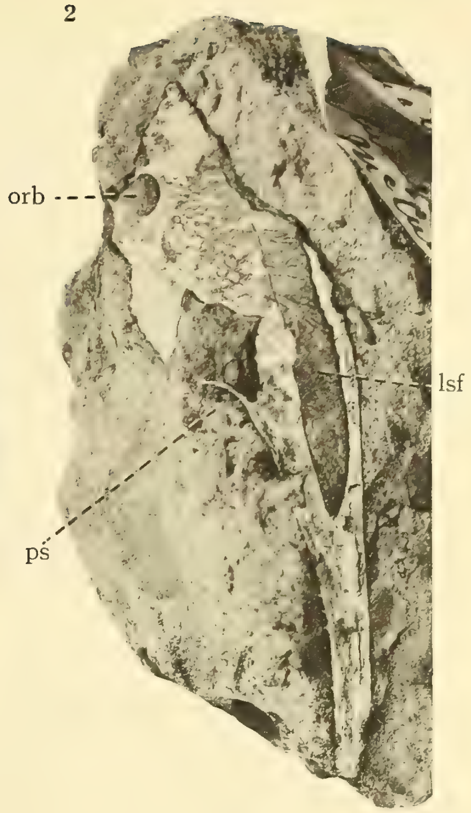

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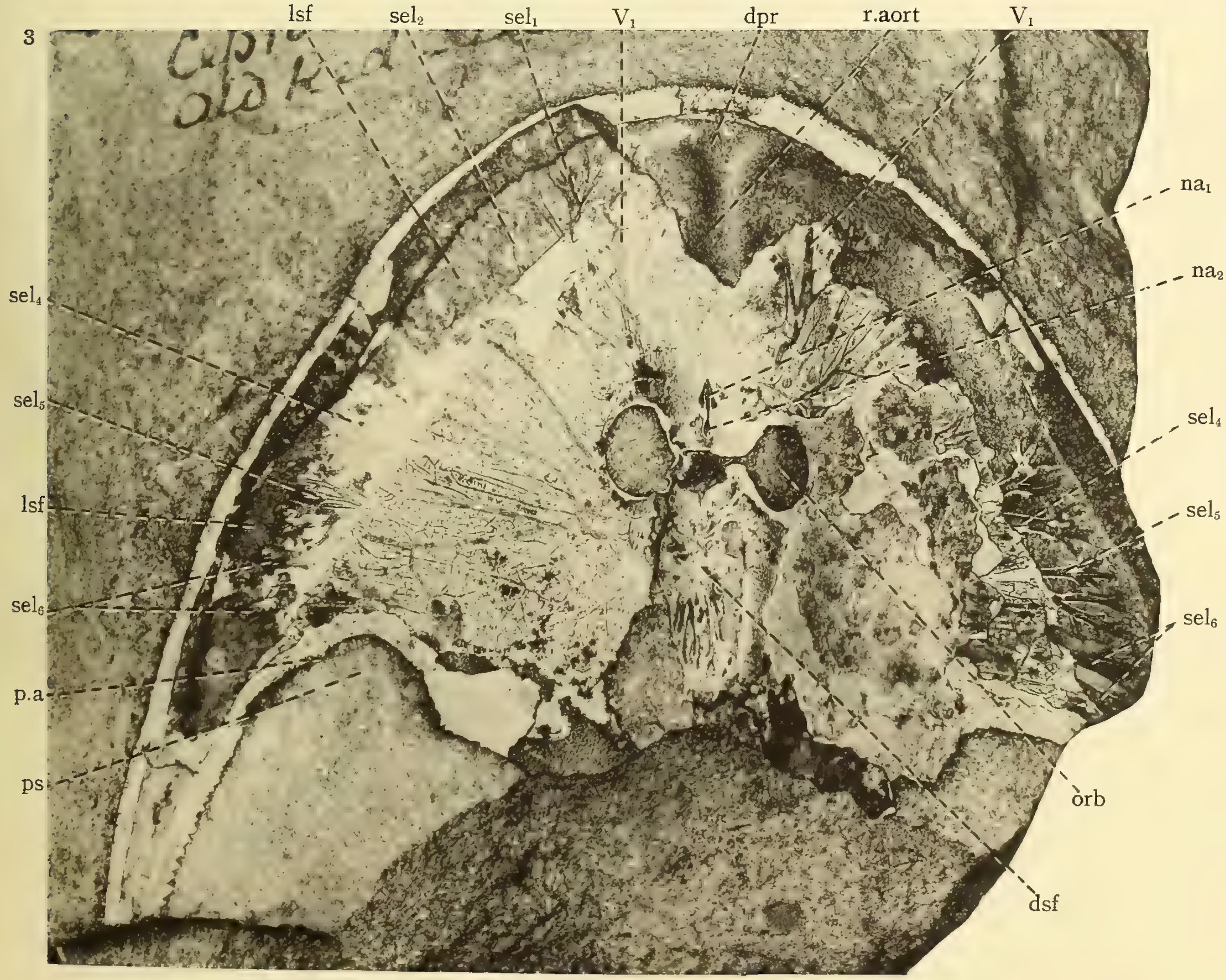

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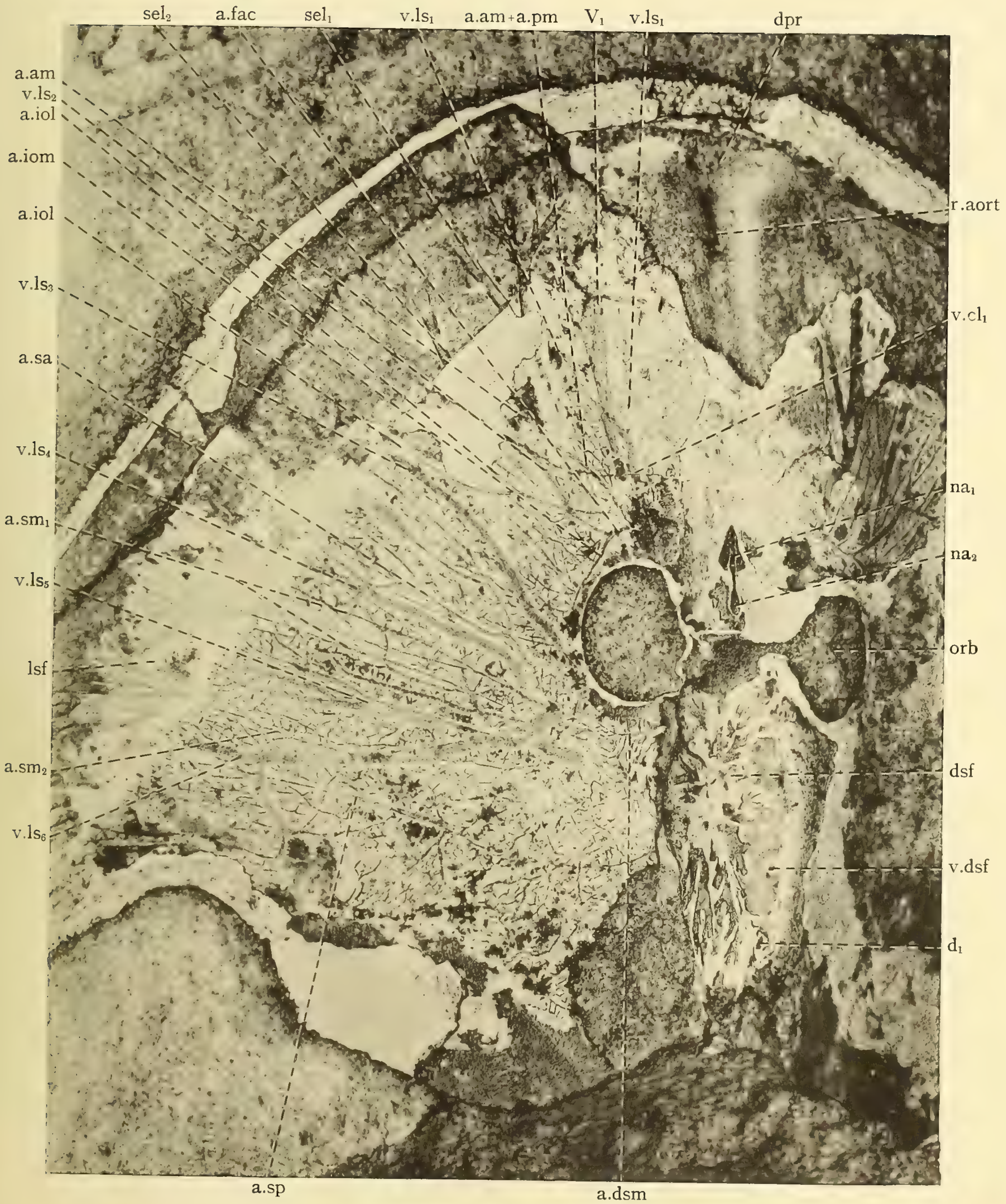
PLATE 21.

Cephalaspis whitei, sp. nov.

Part of cephalic shield magnified to show canals of sub-aponeurotic (sub-cutaneous) vascular plexus. (Same specimen, the Holotype, as in text-fig. 9; Pl. 20, fig. 3; Pl. 32, fig. 6.) × 3½ diam.

a.am, supposed canal of mandibular branch of a. facialis; *a.dsm,* canal of a. superficialis post-orbitalis; *a.fac,* canal of a. facialis; *a.iol,* lateral infra-orbital branch of canal of a. facialis; *a.iom,* canal of medial infra-orbital branch of a. facialis; *a.pm,* canal of pre-mandibular branch of a facialis; *a.sa,* $a.sm_1$, $a.sm_2$, *a.sp,* canals of dorso-lateral superficial arteries 1–4; d_1, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf,* dorsal electric field; *dpr,* impression of supra-oral field; *lsf,* lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb,* orbital opening; *r.aort,* impression of aortic ridge; sel_1, sel_2, canals of 1st and 2nd nerves of lateral electric field; $v.cl_1$, pre-orbital division of canal of v. capitis lateralis; *v.dsf,* canal probably for vein from dorsal electric field; $v.ls_1$–$v.ls_6$, canals of dorso-lateral superficial veins 1–6; V_1, canal of n. profundus.



CEPHALASPIS

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PLATE 22.

Cephalaspis fletti, sp. nov.

FIG. 1.—Cephalic shield doubtfully referred to this species, lateral view. (Same specimen as in Pl. 18, fig. 2.) × 2 diam.

FIG. 2.—Cephalic shield, from left side. (Same specimen, the HOLOTYPE, as in Pl. 15, fig. 3.) × 1½ diam.

Cephalaspis agassizi Lankester.

FIG. 3.—Cephalic shield, from left side. Lower Old Red Sandstone: near Ludlow,* Shropshire. British Museum [no. **33319**.—A. Marston Coll., 1858]. Nat. size.

FIG. 4.—Part of exoskeleton at side of dorsal spine of same specimen, showing ornamentation. × 3 diam.

Hemicyclaspis murchisoni (Egerton), var. *ludlowensis* nov.

FIG. 5.—Cephalic shield, dorsal view. The exoskeleton of the dorsal side has to a large extent been split off. (Counterpart of HOLOTYPE: see Pl. 10, fig. 1.) Museum of Practical Geology, London [no. **47806**.—R. Lightbody Coll.]. × 2 diam.

Cephalaspis pagei Lankester.

FIG. 6.—Part of scale-covered division of left side of trunk, preserved mainly in impression. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.171**.—J. Powrie Coll.]. ×3 diam.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

FIG. 7.—Cephalic shield doubtfully referred to this form. The dorsal exoskeleton is seen from the inside. (See also Pl. 41, fig. 1.) Lower Old Red Sandstone: Kinblythmont, Forfarshire. British Museum [no. **50003**.—W. C. Trevelyan Bequest, 1879]. × 1½ diam.

c.sem.ant, *c.sem.post*, divisions of labyrinth cavity for anterior and posterior semicircular canals respectively; D_2, posterior dorsal fin; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *d.sp*, dorsal spine; *ls*, lateral scales; *lsf*, lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *pin*, pineal opening on dorsal side of endoskeleton of cephalic shield; pin_2, pineal opening in pineal plate; *Ppl*, pineal plate; *ps*, pectoral sinus; sel_1–sel_3, sel_6, canals of nerves 1–3 and 6 of lateral electric field; $v.cl_1$, canal of pre-orbital division of v. capitis lateralis; $v.ls_1$, $v.ls_5$, $v.ls_6$?, canals of dorso-lateral superficial veins 1, 5 and probably also 6; *v.rs*, ventro-lateral scales (N.B. these scales display their ventral surface well); *vs*, ventral scales; V_1, canal of n. profundus.

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* See p. 200.

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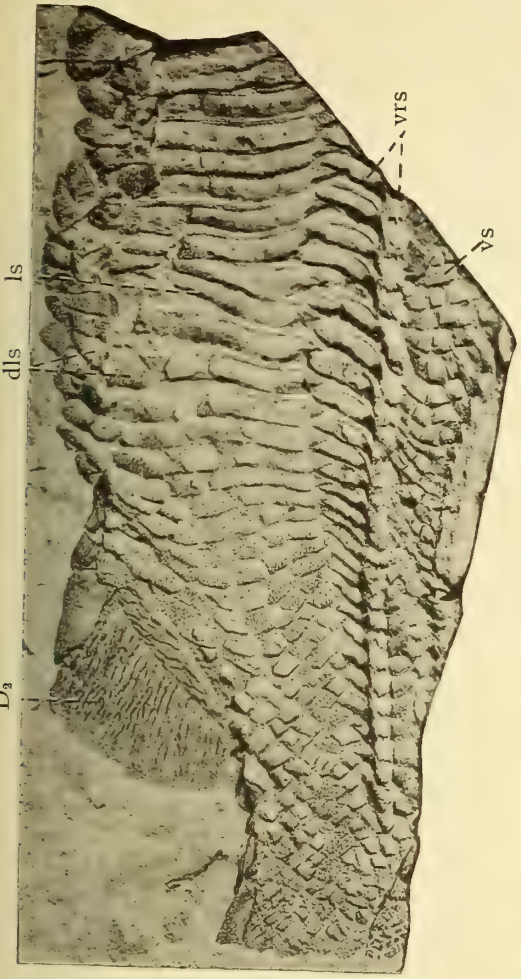

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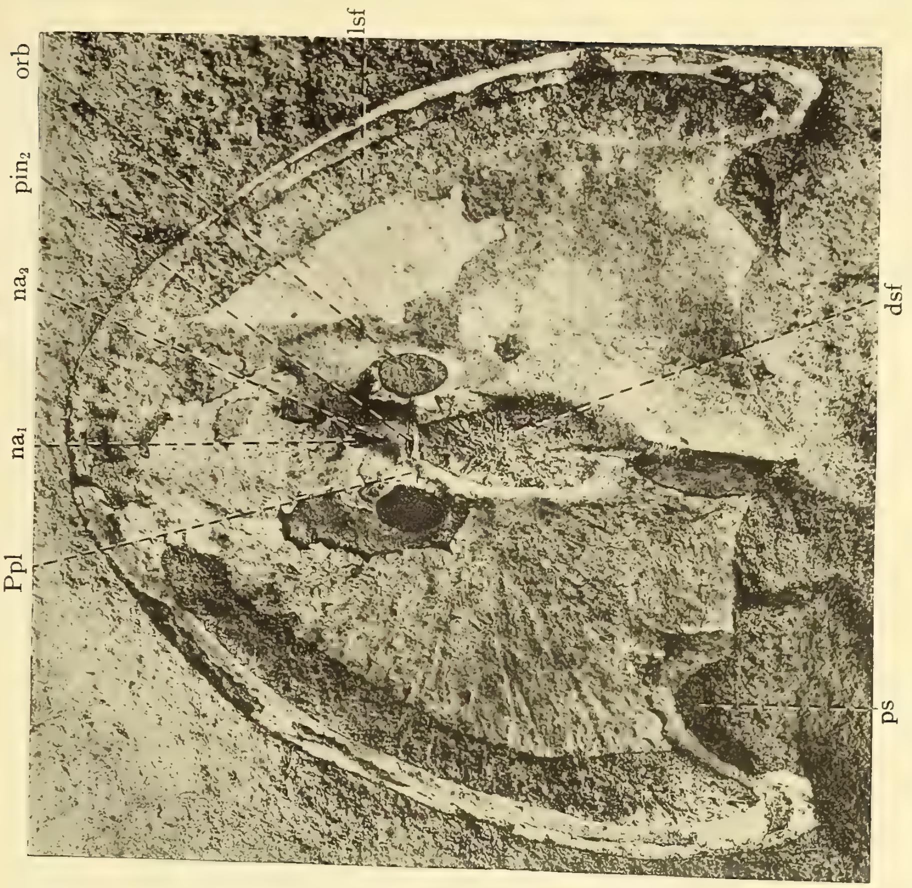

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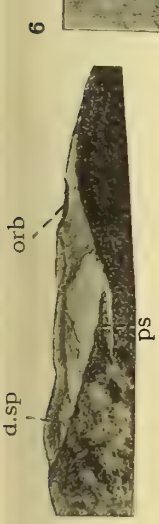

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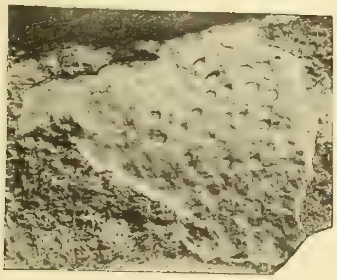

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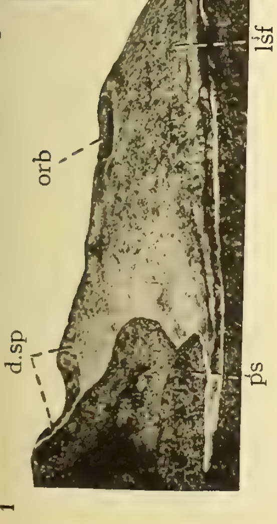

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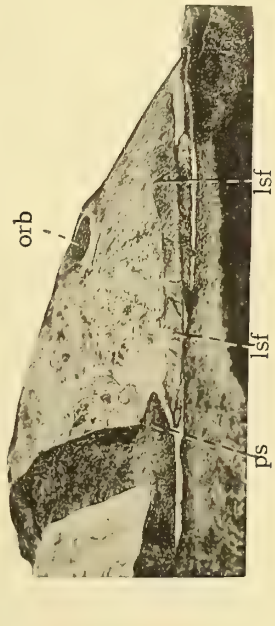

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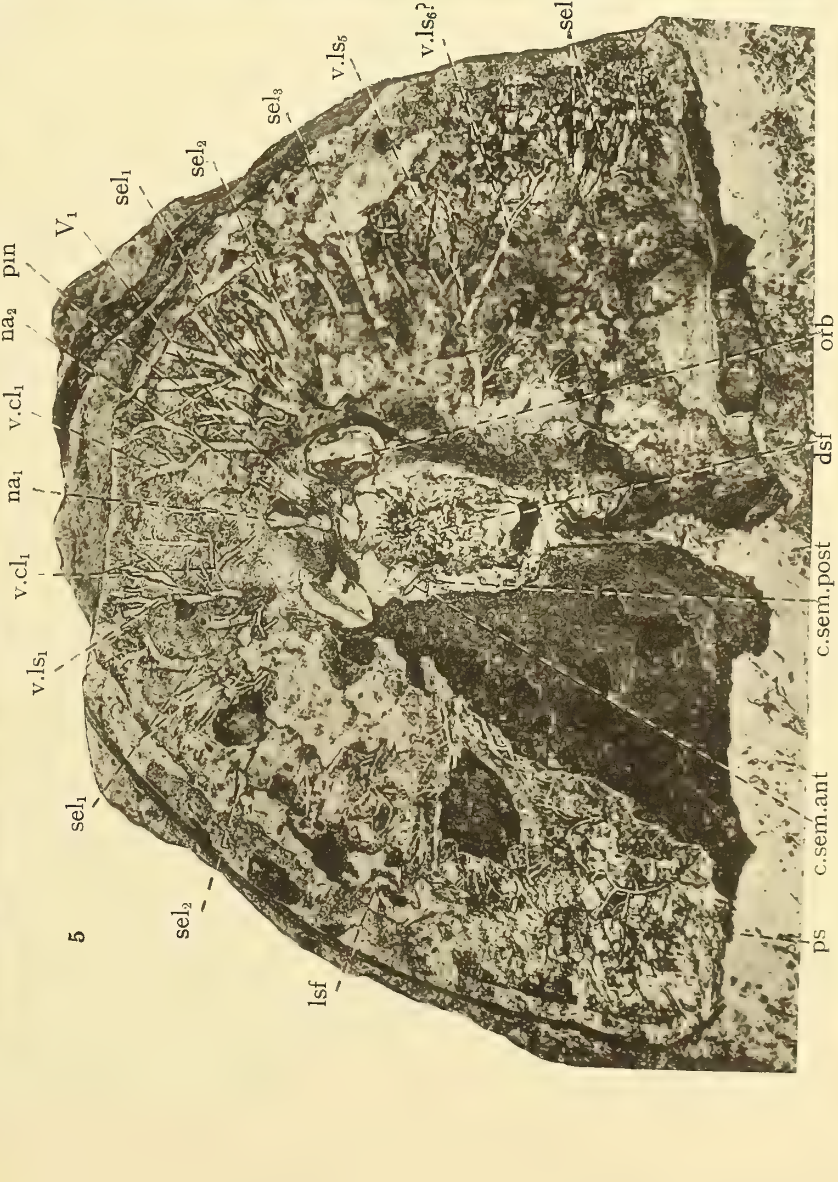

CEPHALASPIS and HEMICYCLASPIS

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PLATE 23.

Cephalaspis sp.

FIG. 1.—Dorsal exoskeleton of cephalic shield, ventral view. (See also Pl. 56, fig. 3.) Lower Old Red Sandstone: Sidlaw (*sic*): Forfarshire. Museum of Practical Geology, London [no. **47813**.—J. Powrie Coll.]. × 2 diam.

Cephalaspis pagei Lankester.

FIG. 2.—Cephalic shield doubtfully referred to this species, dorsal view. The exoskeleton of the dorsal side is partly destroyed. (See also Pl. 59, fig. 1.) Lower Old Red Sandstone: loc. uncertain, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1895.147.5**]. × 2 diam.

Cephalaspis traquairi, sp. nov.

FIG. 3.—Cephalic shield, dorsal view. The exoskeleton of the dorsal side is almost entirely wanting. Lower Old Red Sandstone: Tulloch Quarry, Galston Moor, Ayrshire. HOLOTYPE. Royal Scottish Museum, Edinburgh [no. **1902.23**]. × 2 diam.

dsf, dorsal electric field; *d.sp,* dorsal spine; *iac,* inter-areal mucous canals; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac) na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb,* orbital opening; *pd,* pineal depression; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps,* pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field.

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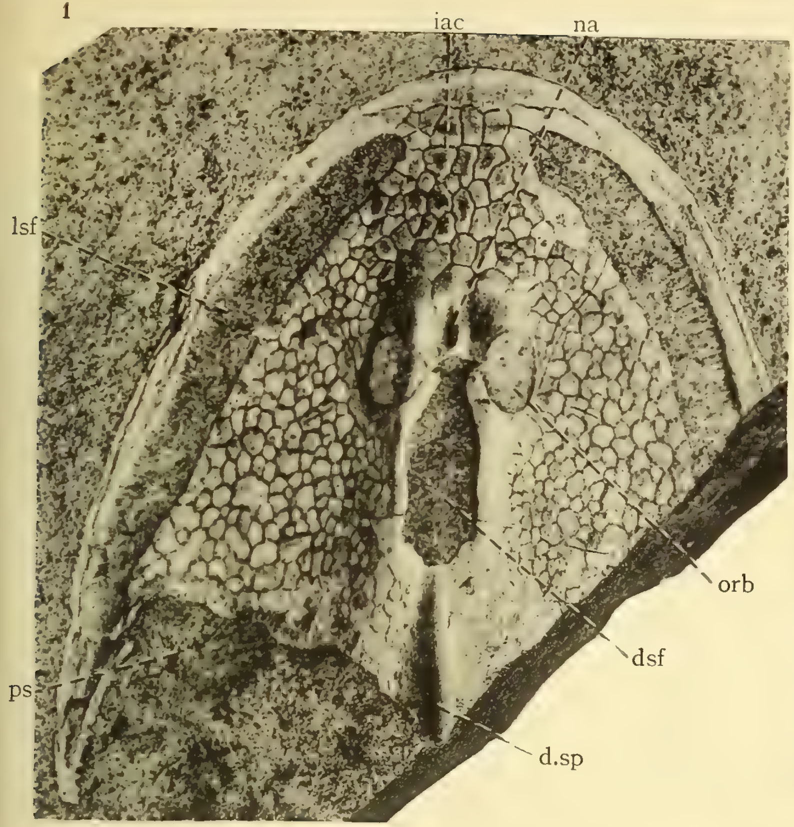

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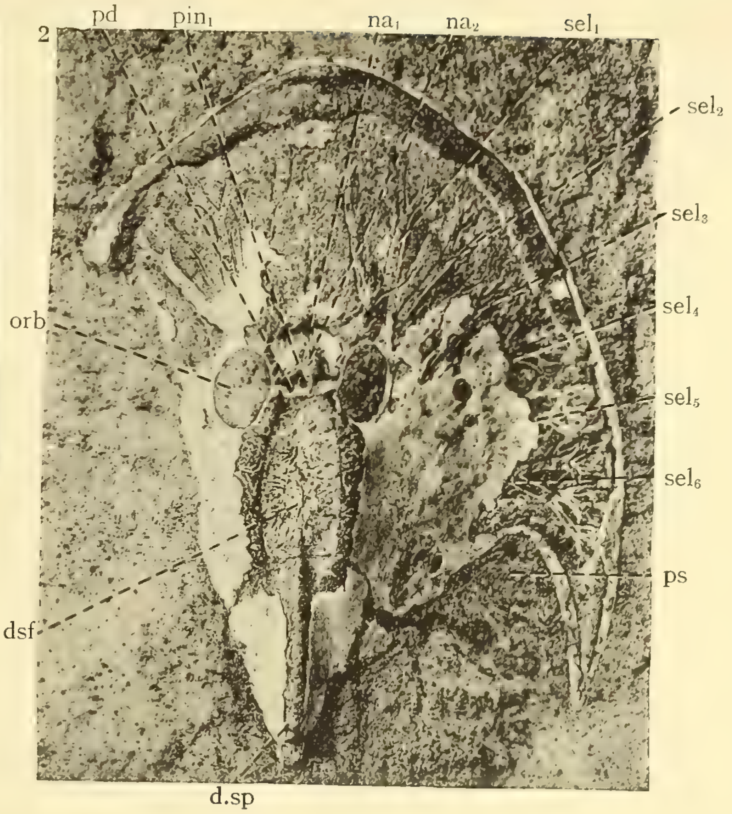

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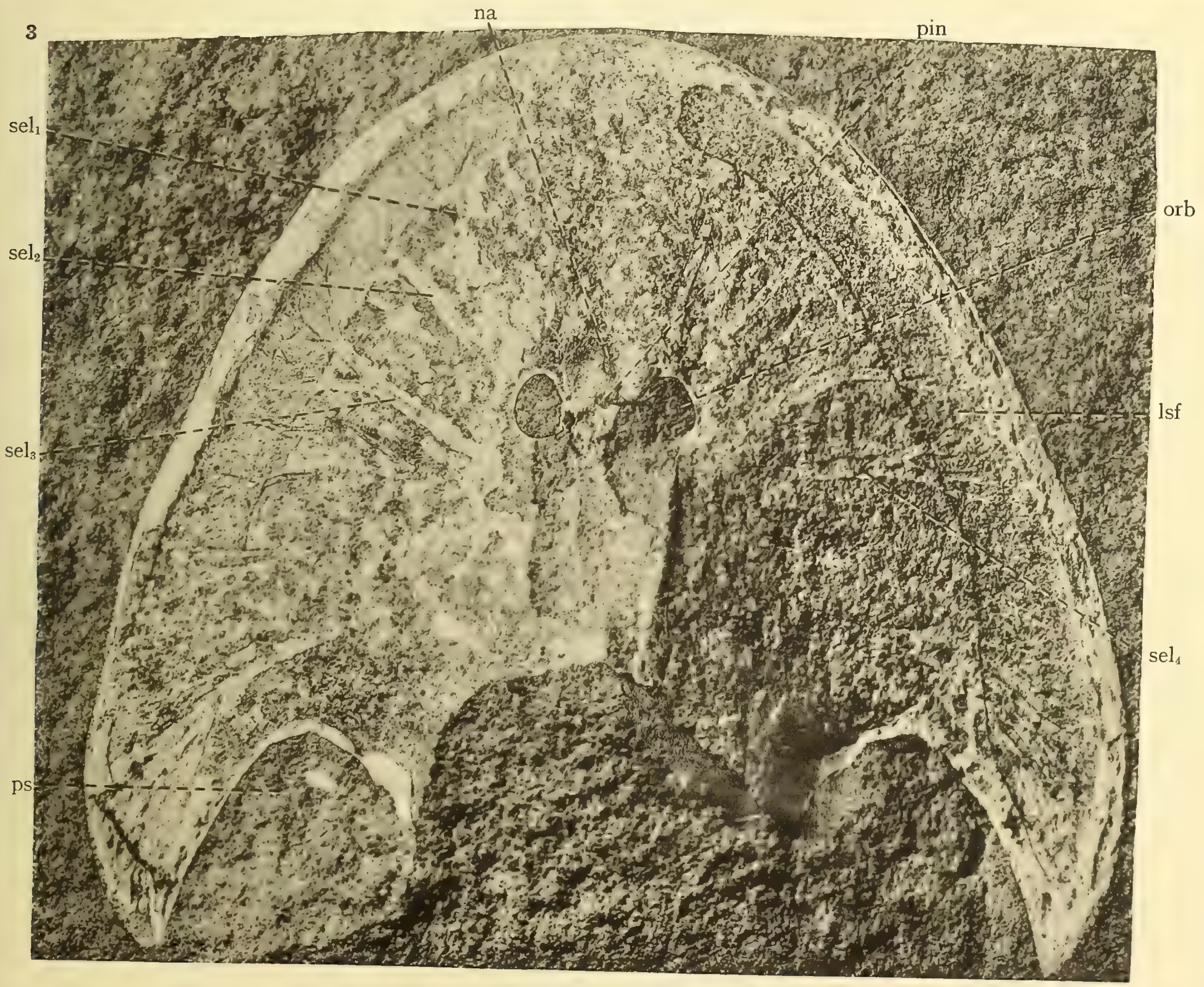

CEPHALASPIS

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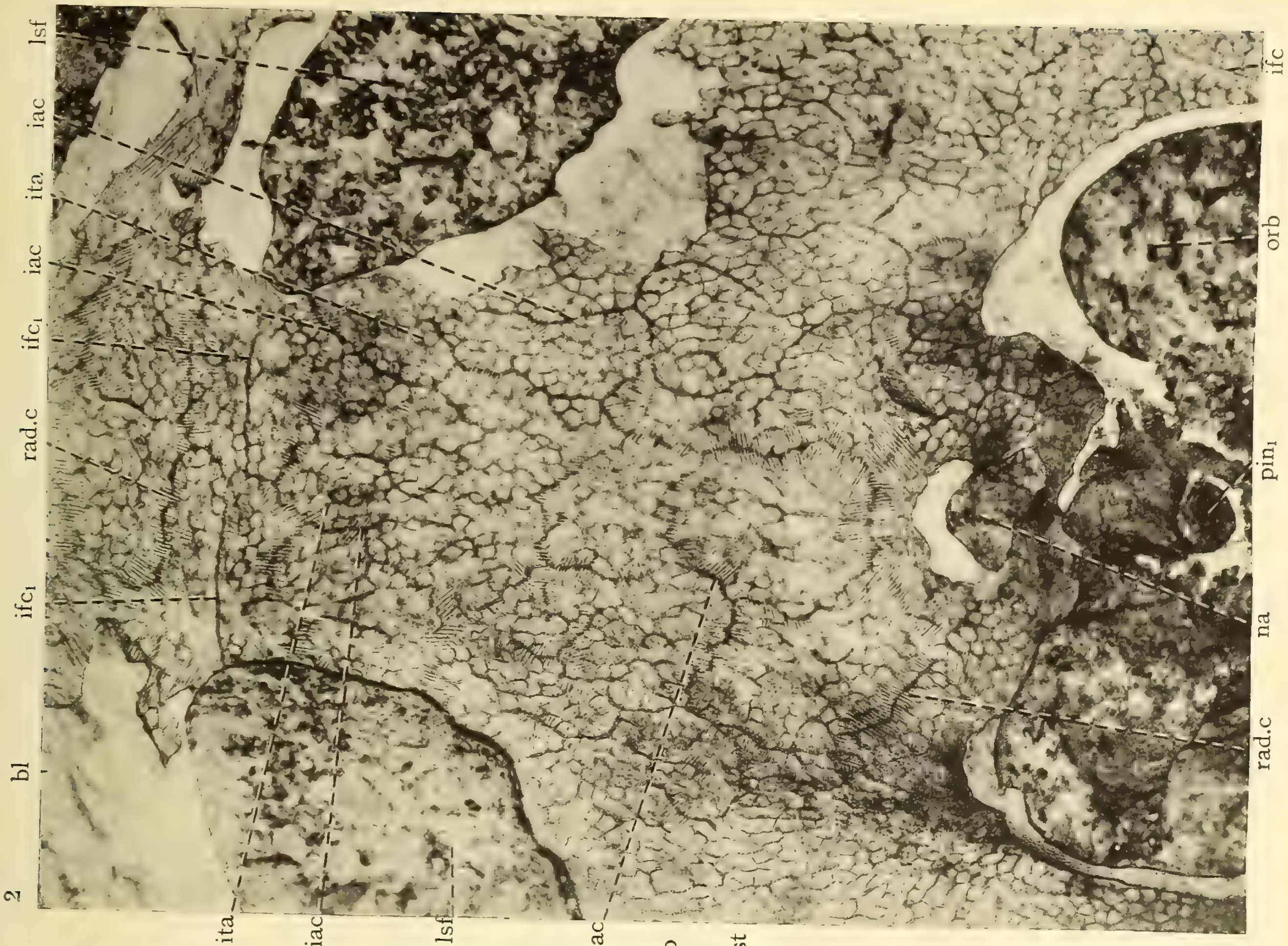
PLATE 24.

Cephalaspis sp.

FIG. 1.—Dorsal exoskeleton and parts of endoskeleton of cephalic shield, ventral view. The basal parts of the exoskeleton are destroyed, thus exposing the mucous canal system. Lower Old Red Sandstone: loc. uncertain, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.182.**—J. Powrie Coll.]. × 3 diam.

FIG. 2.—Anterior part of same specimen more highly magnified to show in detail the disposition of the mucous canal system. × 8 diam.

bl, basal layer of exoskeleton; *cmm*$_2$, ventral-lateral part of sensory canal groove, corresponding either to posterior head-line of pit-organs or to supra-temporal cross-commissure of fishes; *iac*, inter-areal mucous canals; *ifc*, infra-orbital sensory canal groove; *ifc*$_1$, anterior part of infra-orbital sensory canal groove, probably corresponding to supra-orbital sensory canal of fishes; *ita*, intra-areal mucous canals; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *pin*$_1$, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; *rad.c*, radiating canals; ***vest***, vestibular division of labyrinth cavity.



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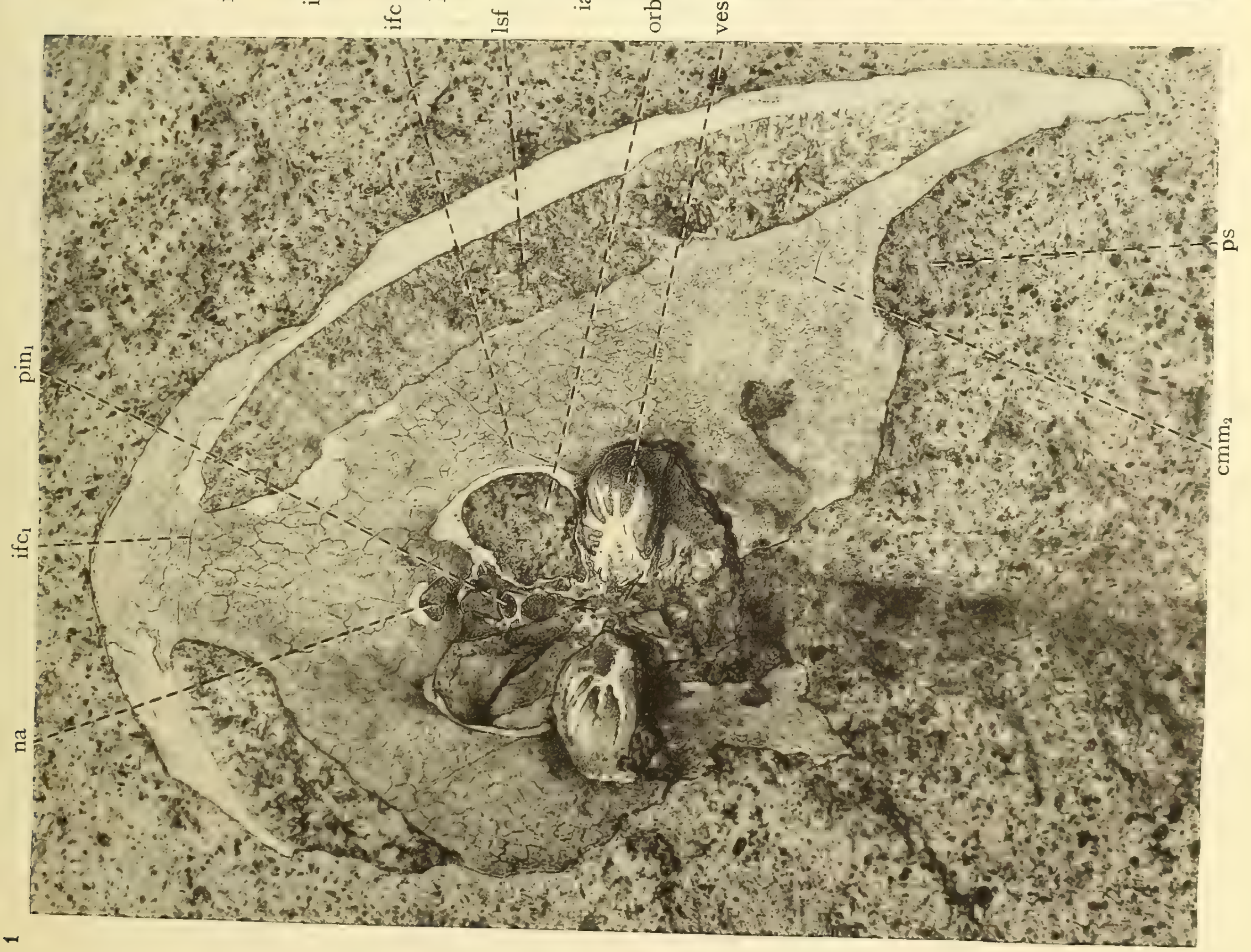

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PLATE 25.

Cephalaspis salweyi Egerton.

Fig. 1.—Cephalic shield, dorsal view. This specimen is prepared to show the labyrinth cavity and the cast of the anterior half of the oralo-branchial chamber. Lower Old Red Sandstone: Heightington, Worcestershire. British Museum [no. **P. 189.**—Weaver Jones Coll., 1880]. Nat. size.

Cephalaspis sollasi, sp. nov.

Fig. 2.—Cephalic shield, dorsal view. The entire dorsal exoskeleton of the shield has been weathered away. Lower Old Red Sandstone: Cradley, Herefordshire. Holotype. University Museum, Oxford [not numbered.—R. B. Grindrod Coll., 1882]. Approx. nat. size.

Cephalaspis powriei Lankester, forma typica.

Fig. 3.—Fairly complete specimen doubtfully referred to this form, dorsal view. Lower Old Red Sandstone: Middleton Quarries, Forfarshire. Bay. Sammlung f. Pal. u. hist. Geol., Munich [not numbered]. Nat. size.

a.car, canal of a. carotis; *a.eff*$_1$, groove of a. branchialis efferens 1 (impression and therefore appearing as a ridge); *a.iol,* canal of lateral infra-orbital branch of a. facialis (impression only); *a.rostr,* groove of a. rostralis (impression and therefore appearing as a ridge); *C,* caudal fin; *c.sem.post,* division of labyrinth cavity for c. semicircularis posterior; D_2, posterior dorsal fin; *des,* canal of electric nerve of dorsal electric field; *dpr,* cast of supra-oral field; *dsf,* dorsal electric field; *ibr*$_1$, inter-branchial ridge 1 (approximately at transition into inter-branchial septum 1); k_3 branchial fossa; k_1–k_3, casts of branchial fossae 1–3; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; *orb,* orbital opening; *pin*$_1$, pineal opening on dorsal side of endoskeleton of cephalic shield; *orb,* orbit; *pr.orb,* orbital prominence on roof of oralo-branchial chamber; *ps,* pectoral sinus; *r.aort,* impression of aortic ridge; *r.pm,* impression of pre-branchial ridge; *sel*$_1$–*sel*$_6$, canals of nerves 1–6 of lateral electric field; *v.cl*$_1$, canal of pre-orbital division of v. capitis lateralis; *vest,* vestibular division of labyrinth cavity; *v.ls*$_1$, *v.ls*$_3$, canals of dorso-lateral superficial veins 1 and 3; *vs.r,* openings of rostral vein-sinus; *vv.rs,* rostral veins; V_1, canal of n. profundus; V_2?, supposed canal of n. trigeminus proper; *VII,* canal of a. facialis; *IXa,* canal of n. glossopharyngeus from labyrinth cavity to oralo-branchial chamber.

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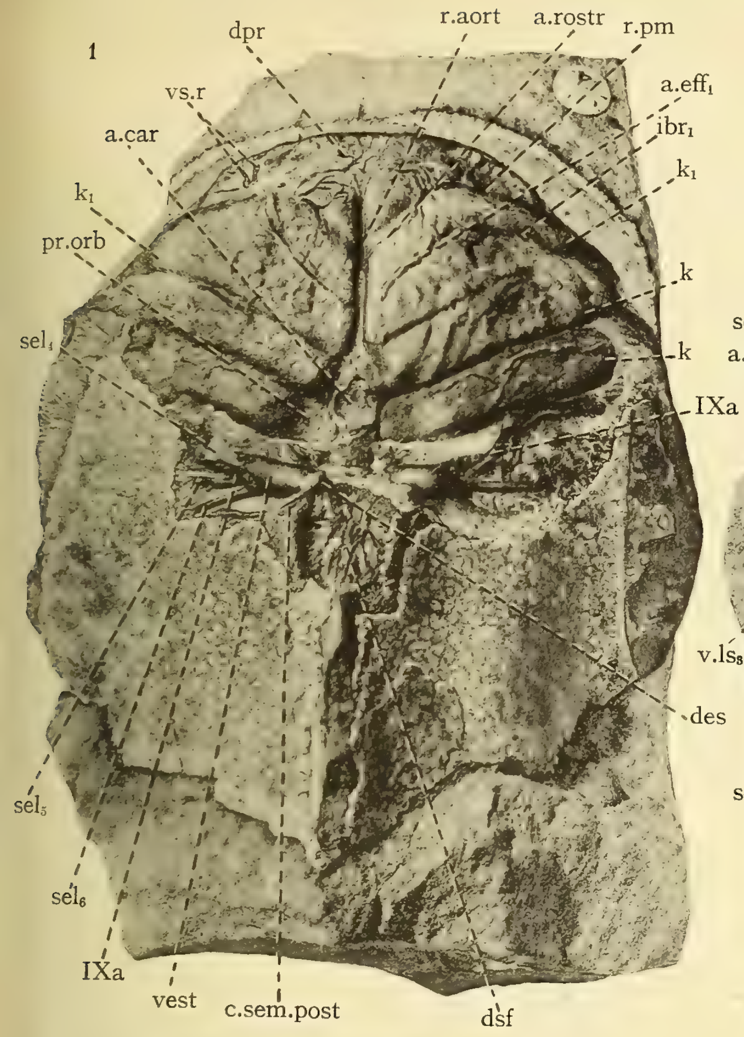

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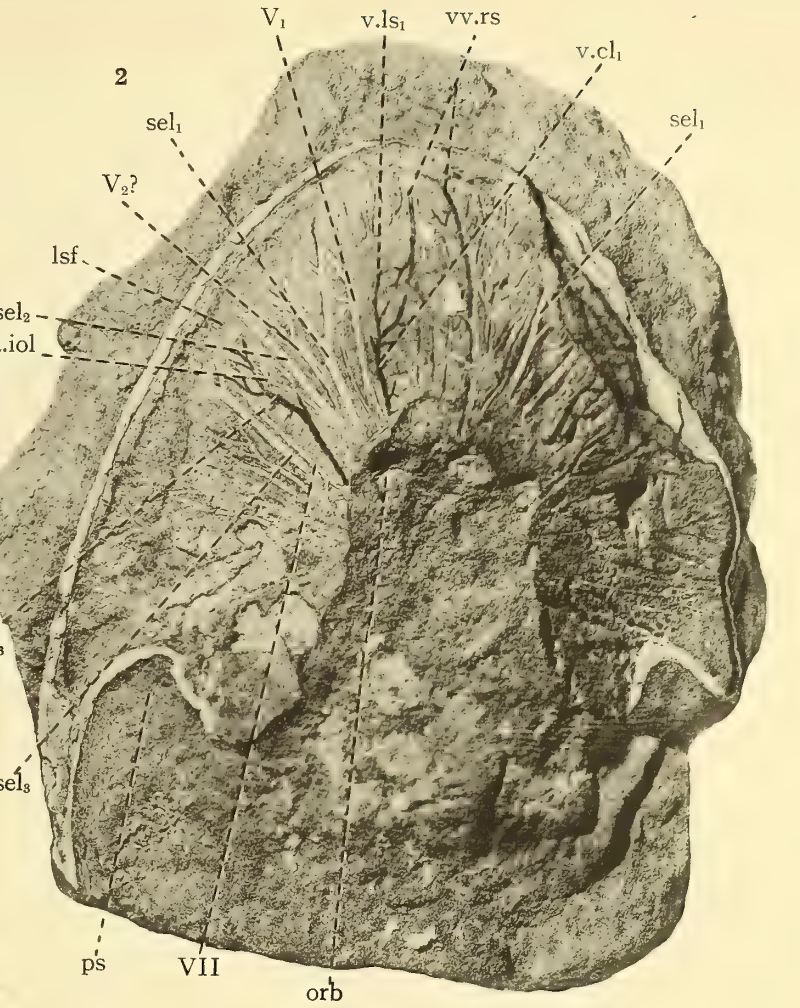

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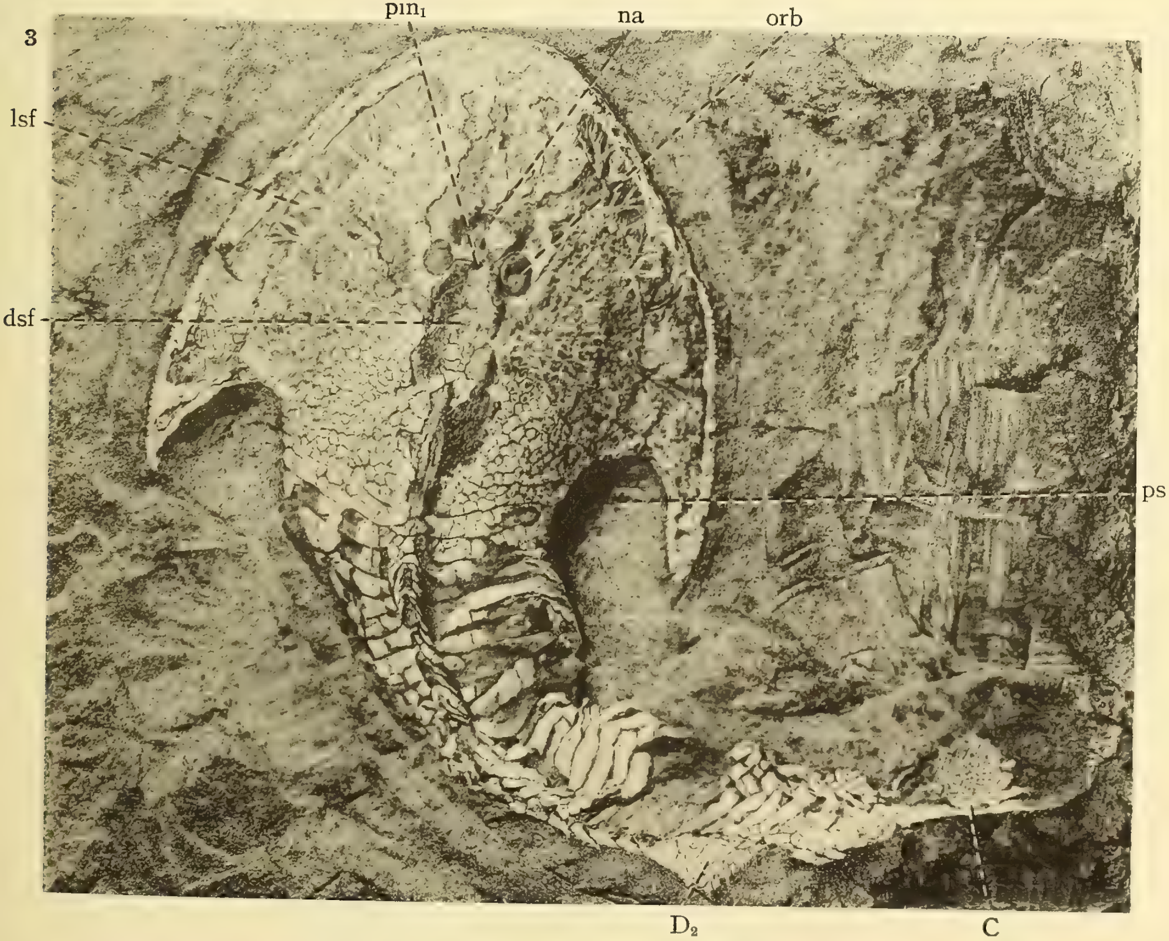

CEPHALASPIS

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PLATE 26.

Cephalaspis sp.

FIG. 1.—Cephalic shield referable to either *C. powriei* var. *asper* or *C. watsoni*, dorsal view. The dorsal exoskeleton of the shield is almost entirely destroyed. Lower Old Red Sandstone: loc. unknown. British Museum [no. **P. 16145.**—Kinnaird Coll., *ex* Coll. Dundee Museum, 1932]. ×1½ diam.

Cephalaspis powriei Lankester, forma typica.

FIG. 2.—Cephalic shield doubtfully referred to this form, dorsal view. Only the basal layer of the dorsal exoskeleton is generally preserved. Specimen figured by Agassiz (1837, Pl. 1*b*, fig. 1—see also Pl. 41, fig. 2). Lower Old Red Sandstone: loc. uncertain, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1932.18**]. × 1½ diam.

a.fac, canal of a. facialis; *a.iol*, canal of anterior lateral infra-orbital branch of a. facialis; *a.iom*, canal of medial infra-orbital branch of a. facialis; *a.sa*, $a.sm_1$, *a.sp*, canals of dorso-lateral superficial arteries 1, 2 and 4; *dsf*, dorsal electric field; *f.cn*, circum-nasal fossa; *lsf*, lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial opening (nasal opening proper); *orb*, orbital opening; *otl*, posterior margin of endoskeleton of otic region, continuous with lateral margin of endoskeleton of occipital region medially, and with medial margin of endoskeletal shoulder-girdle laterally; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field; $v.ls_3$–$v.ls_6$, canals of dorso-lateral superficial veins 3–6.

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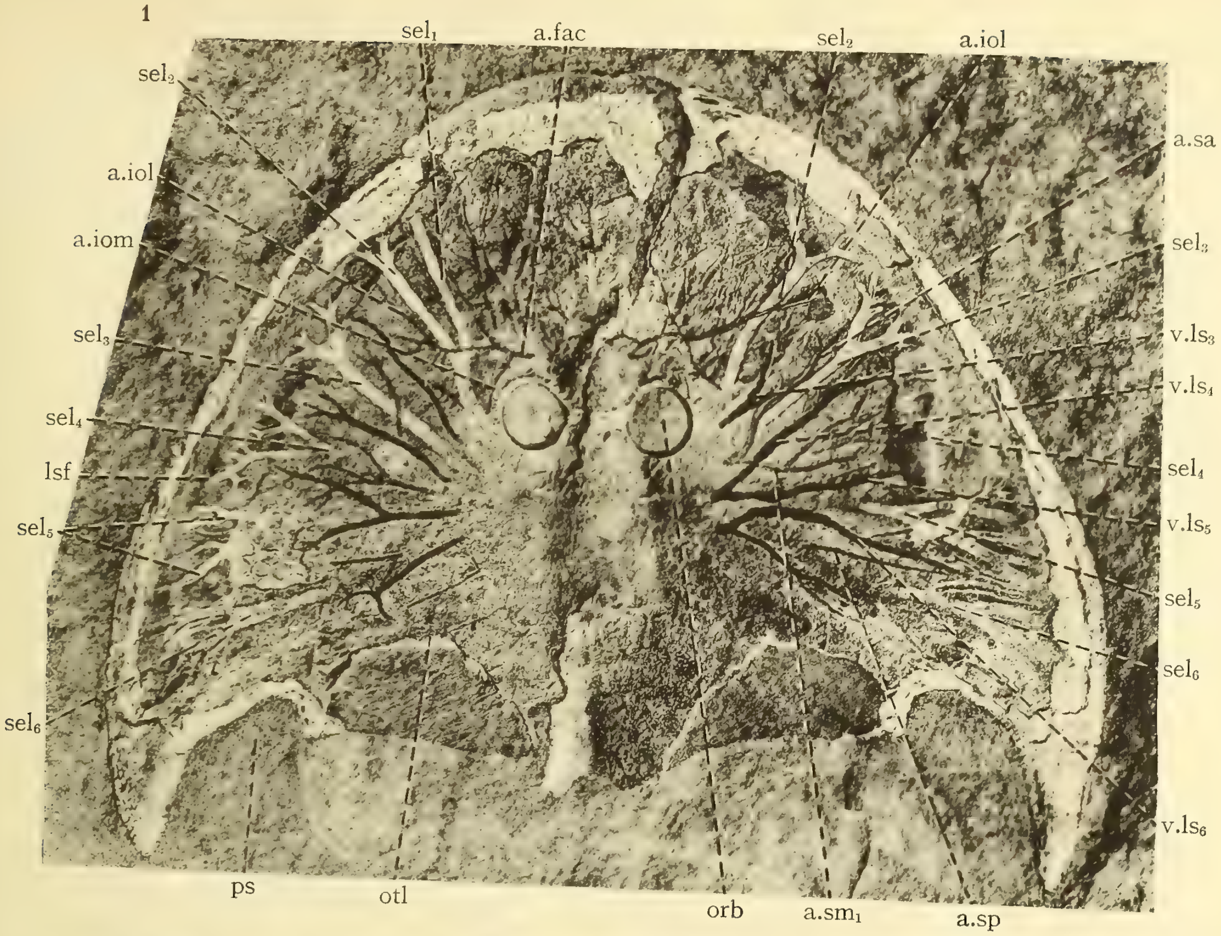

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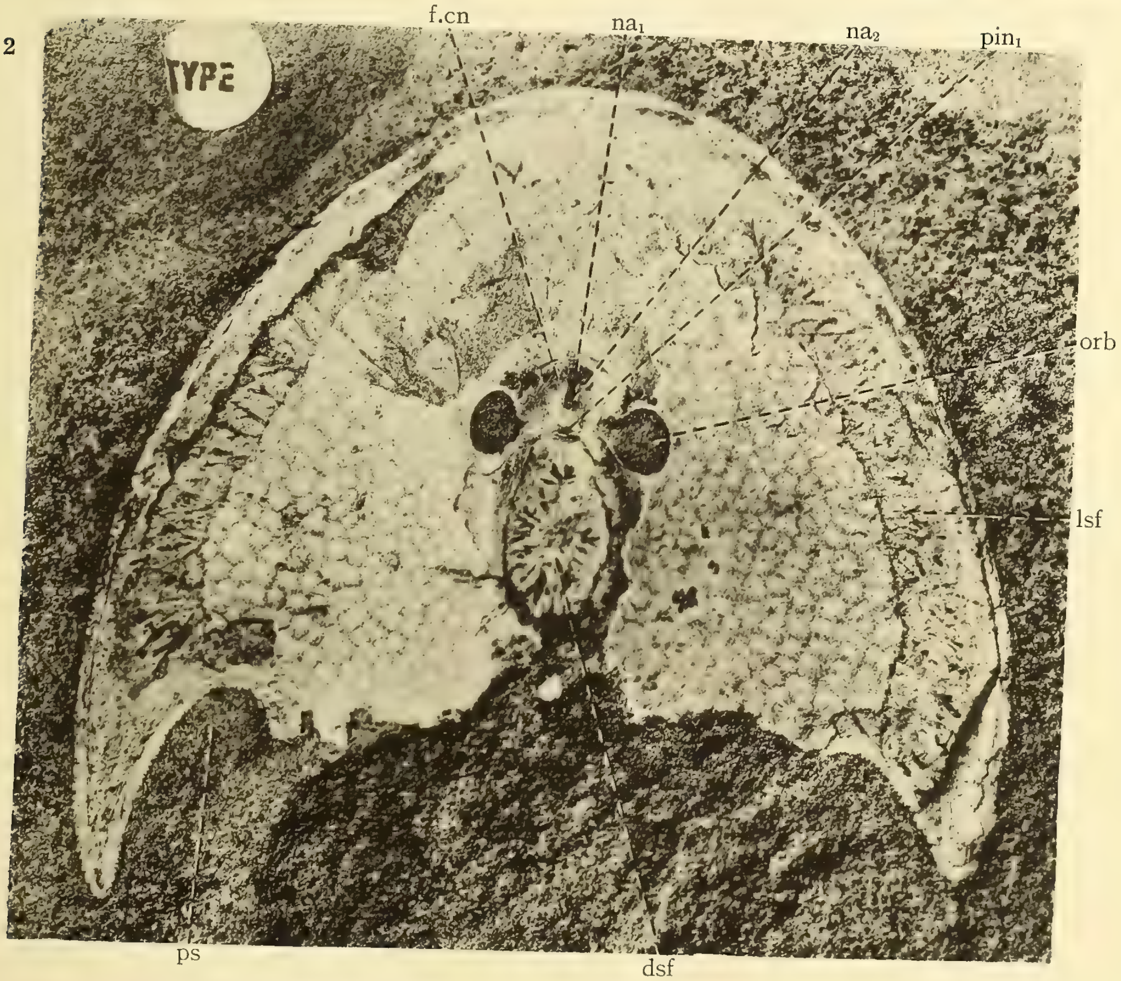

CEPHALASPIS

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PLATE 27.

Cephalaspis powriei Lankester, forma typica.

FIG. 1.—Cephalic shield, dorsal view. (See also fig. 2 and Pl. 44, figs. 2, 3.) Lower Old Red Sandstone: Risk Quarry, Brechin, Forfarshire. LECTOTYPE. Royal Scottish Museum, Edinburgh [no. **1891.92.146.**—J. Powrie Coll.]. × 1½ diam.

FIG. 2.—Counterpart of same specimen. (See also Pl. 32, figs. 2–4.) British Museum [no. **P. 6944.**—Hugh Mitchell Coll., 1893]. × 1½ diam.

Thyestes egertoni (Lankester).

FIG. 3.—Cephalic shield, dorsal view. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 6112.**—G. H. Piper Coll., 1889]. × 2 diam.

FIG. 4.—Imperfect impression of dorsal side of cephalic shield. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 5315.**—G. H. Piper Coll., 1887]. × 2 diam.

Cephalaspis whitei, sp. nov.

FIG. 5.—Right cornu and adjacent parts of exoskeleton of dorsal side of cephalic shield, ventral view. Lower Old Red Sandstone: near Pontrilas,* Herefordshire. British Museum [no. **P. 7168*a*.**—Purchased, 1892]. × 1½ diam.

d_1, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf,* dorsal electric field; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; *orb,* orbital opening; *pin,* pin_1, pineal opening (pin_1, on dorsal surface of endoskeleton of cephalic shield); *ps,* pectoral sinus.

* See p. 200.

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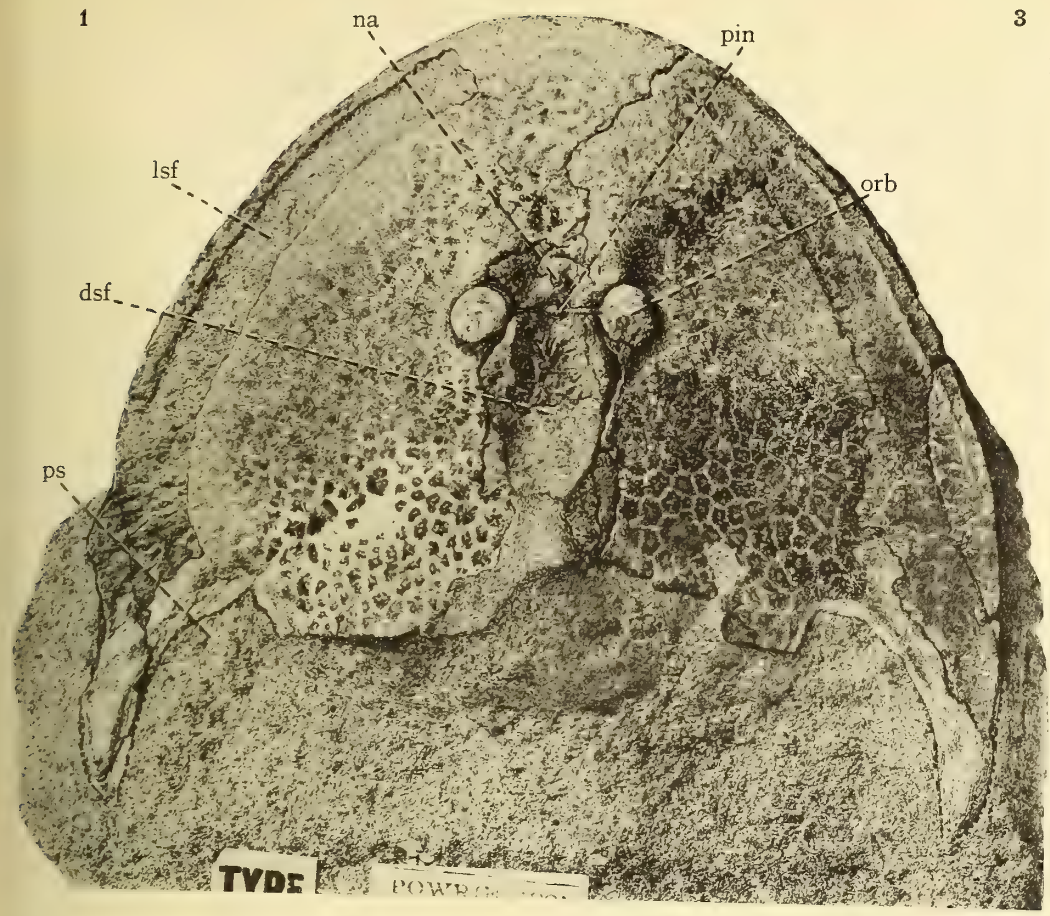

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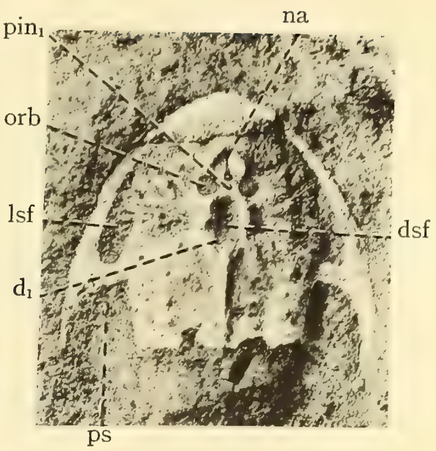

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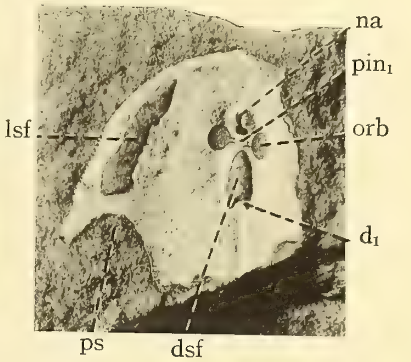

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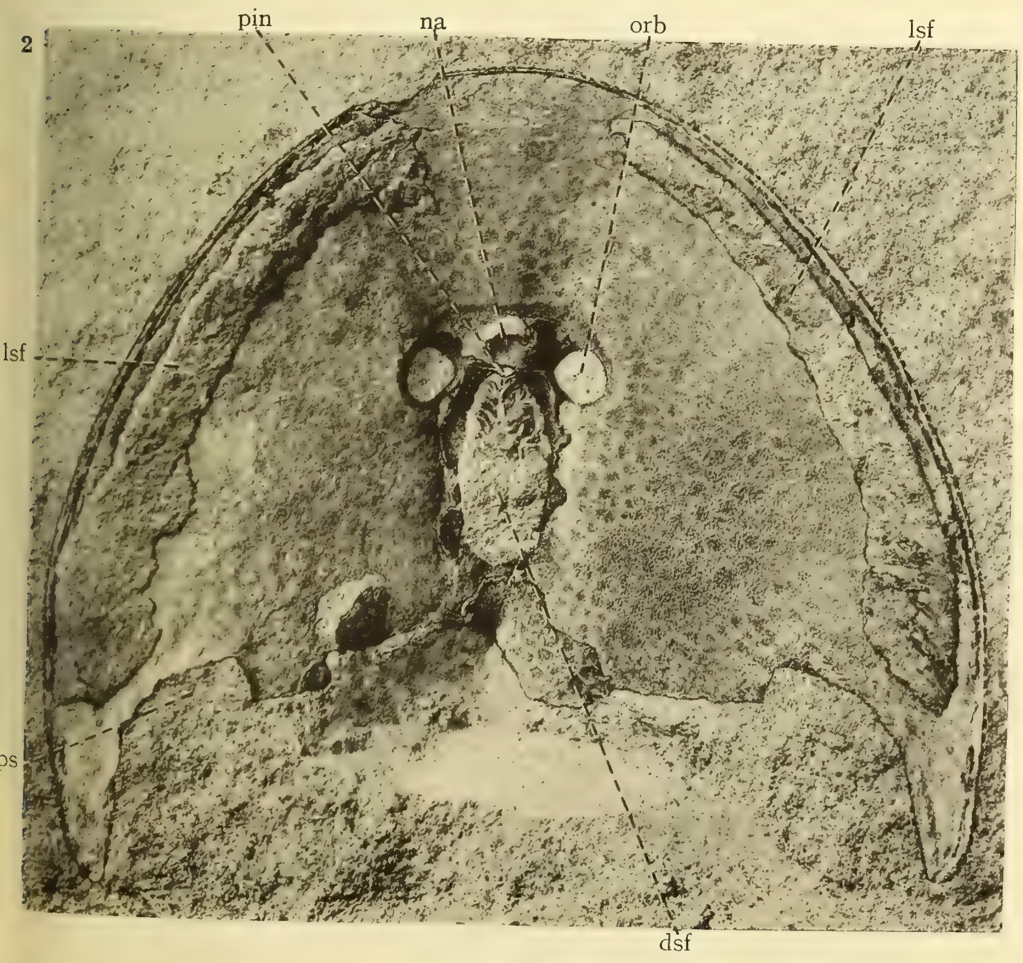

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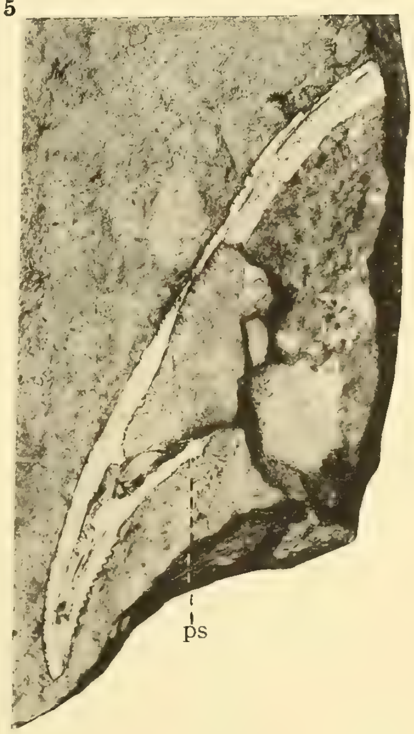

CEPHALASPIS and THYESTES

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PLATE 28.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

FIG. 1.—Cephalic shield, dorsal view. The dorsal exoskeleton is preserved only in a few places; towards the middle of the shield parts have split off, exposing an impression of the roof of the oralo-branchial chamber. Lower Old Red Sandstone: loc. uncertain. British Museum [no. **P. 16144.**—Kinnaird Coll., *ex* Coll. Dundee Museum, 1932]. Nat. size.

FIG. 2.—Cephalic shield, dorsal view. This specimen is preserved similarly to that in fig. 1. Lower Old Red Sandstone: Rossie Priory, Perthshire. Museum of Practical Geology, London [no. **47785.**—Kinnaird Coll.]. Approx. × $1\frac{1}{2}$ diam.

FIG. 3.—Much-flattened specimen doubtfully referred to this variety, dorsal view. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.163.**—J. Powrie Coll.]. Approx. nat. size.

aort.gr, impression of aortic groove on aortic ridge; *dpr*, supra-oral field; *dsf*, dorsal electric field; *ls*, lateral scales; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *Pec*, pectoral fin; *pin*, pineal opening (here probably in the pineal plate); *pr.au*, impression of otic prominence on roof of oralo-branchial chamber; *pr.orb*, impression of orbital prominence on roof of oralo-branchial chamber; *ps*, pectoral sinus; *r.aort*, impression of aortic ridge; *r.pm* ?, supposed pre-branchial ridge; sel_1, sel_3, sel_6, canals of nerves 1, 3 and 6 of lateral electric field; *vrs*, ventro-lateral scales.

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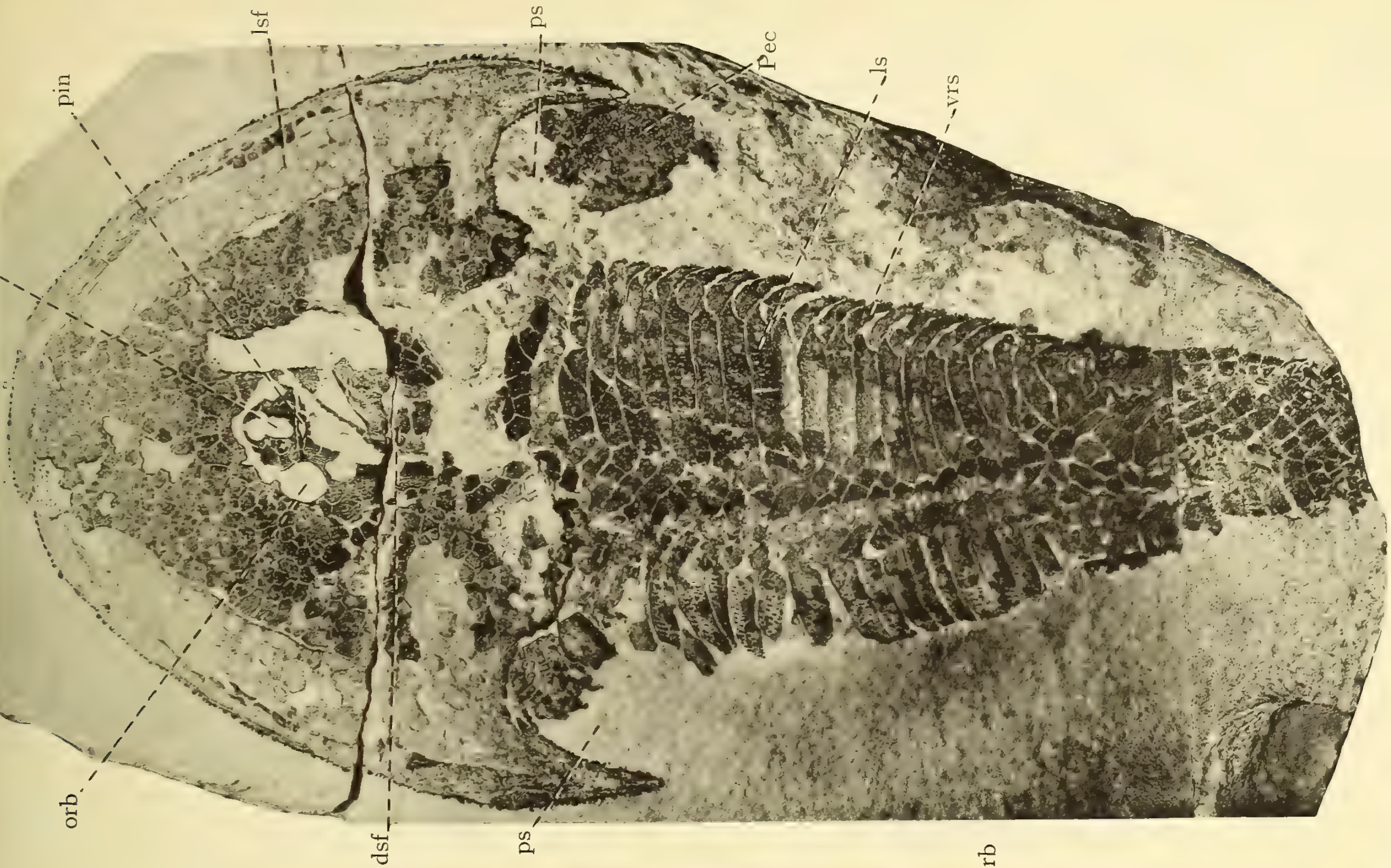

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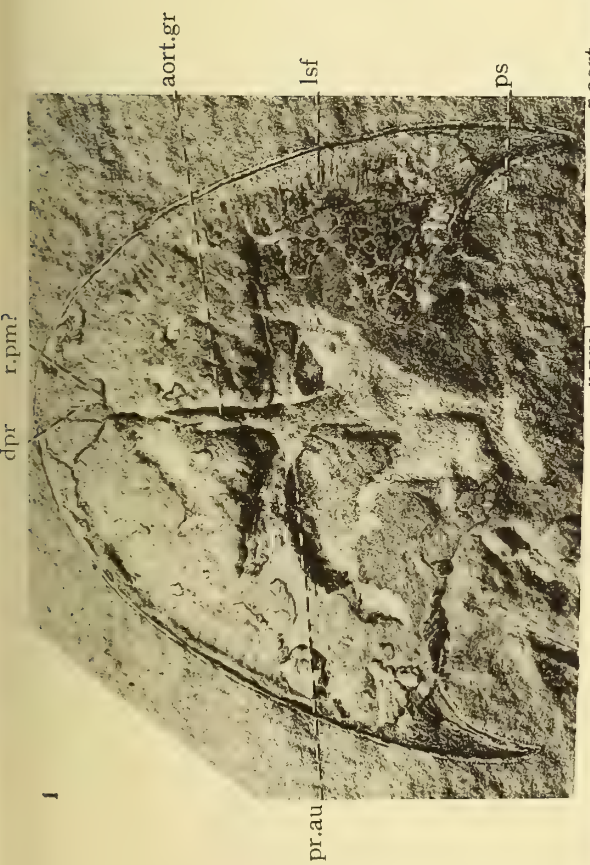

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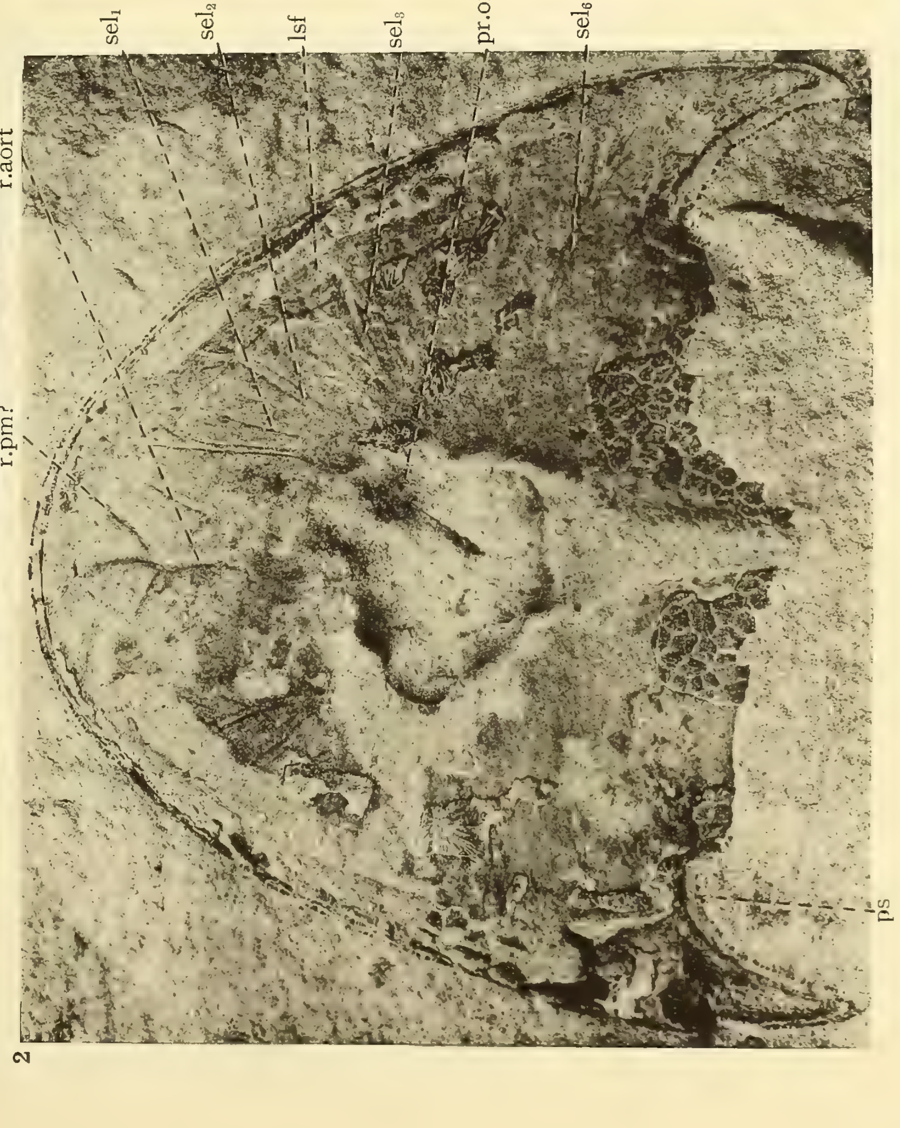

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PLATE 29.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

FIG. 1.—Part of exoskeleton, basal view. The surface has been made transparent by means of xylol in order to show the detailed disposition of the mucous canals. (Same specimen, the HOLOTYPE, as in fig. 3.) × 17 diam.

FIG. 2.—Right cornu, ventral view. Specimen made transparent by means of xylol. (Same specimen, the HOLOTYPE, as in fig. 3.) × 3 diam.

FIG. 3.—Dorsal exoskeleton of cephalic shield, in ventral view. Lower Old Red Sandstone : Turin Hill, Forfarshire. HOLOTYPE. Museum of Practical Geology, London [no. **47819.**—J. Powrie Coll.]. × $1\frac{1}{2}$ diam.

ebc, external branches of radiating canals passing upwards between meshes formed by mucous canals; *iac*, inter-areal canals; *ifc*, infra-orbital sensory canal groove; ifc_1, anterior portion of infra-orbital sensory canal groove, probably corresponding to supra-orbital sensory canal of fishes; *ita*, intra-areal mucous canals; *lsf*, lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *ps*, pectoral sinus; *rad.c*, radiating canals of middle layer of exoskeleton.

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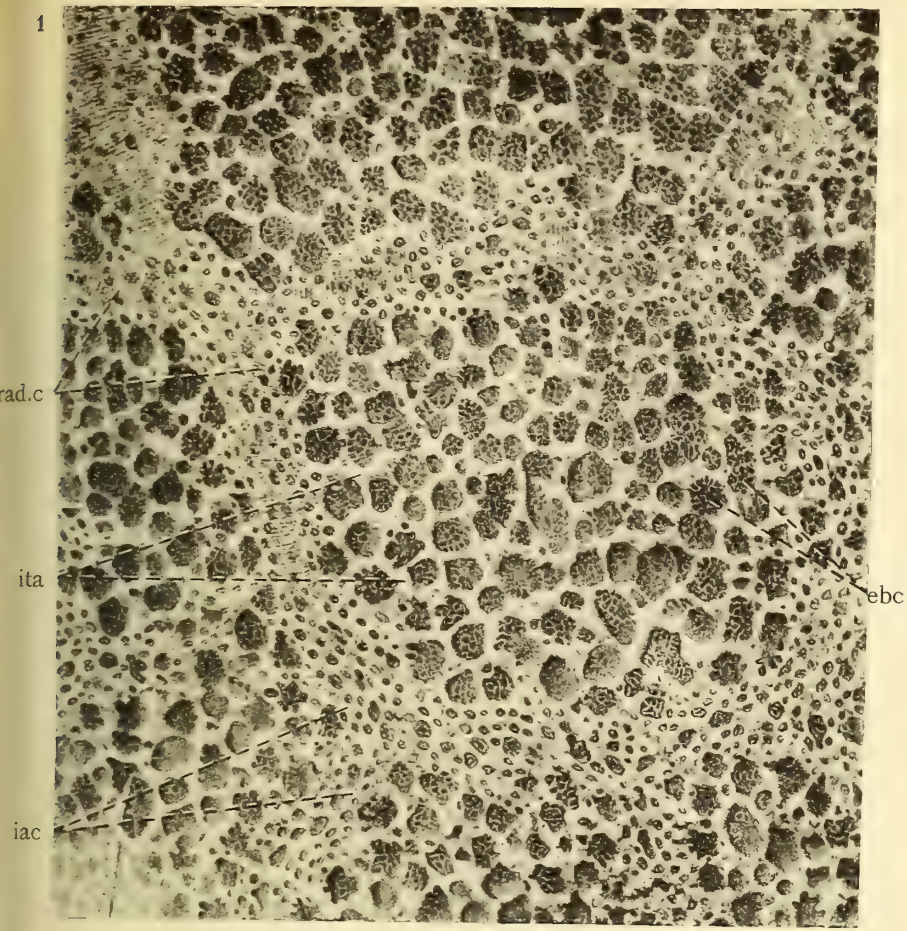

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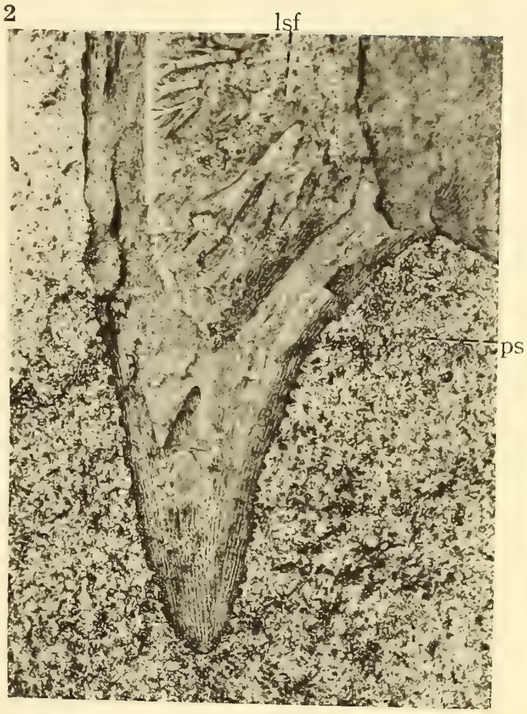

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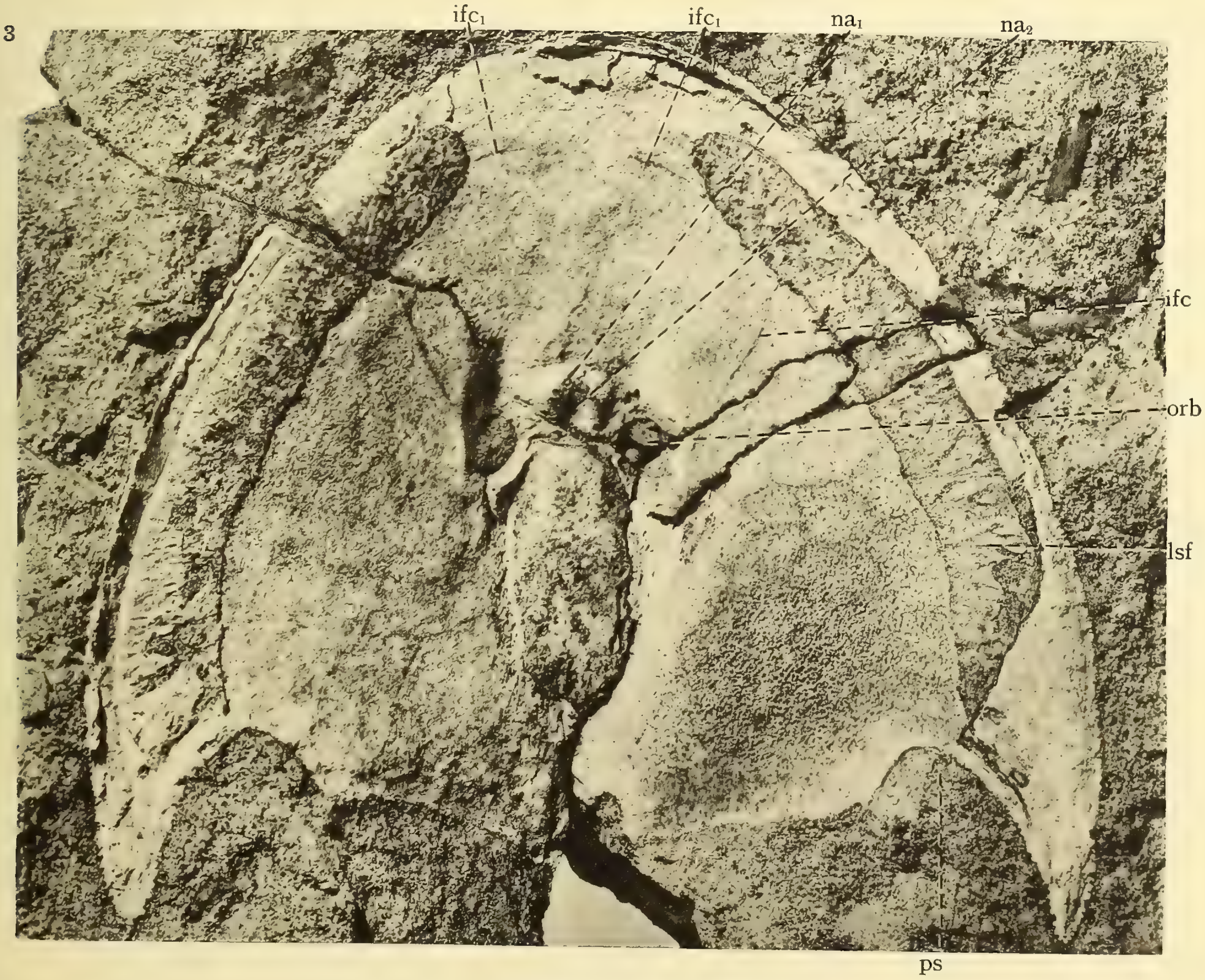

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PLATE 30.

Cephalaspis powriei Lankester, var. *asper* Lankester.

Fig. 1.—Flattened specimen lacking posterior half of trunk, dorsal view. Lower Old Red Sandstone: loc. uncertain, Forfarshire. British Museum [no. **P. 671.**—P. M. G. Egerton Coll., 1882]. Nat. size.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

Fig. 2.—Flattened cephalic shield, dorsal view. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.158***a*.—J. Powrie Coll.]. Nat. size.

Cephalaspis powriei Lankester, var. *asper* Lankester.

Fig. 3.—Dorsal exoskeleton of cephalic shield with a few scales, ventral (internal) view. Lower Old Red Sandstone: Turin Hill, Forfarshire. LECTOTYPE. Royal Scottish Museum, Edinburgh [no. **1891.92.161.**—J. Powrie Coll.]. Nat. size.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

Fig. 4.—Specimen doubtfully referred to this variety, showing postero-lateral part of dorsal exoskeleton of cephalic shield with pectoral fin and adjacent parts of squamation, ventral view. (Part of same specimen as in Pl. 43, fig. 2.) × 3 diam.

d_1, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf*, dorsal electric field; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *Pec*, pectoral fin; pin_2, pineal opening (in the pineal plate?); *Ppl*, pineal plate (?); *ps*, pectoral sinus; *sd.cr*, scutes of dorsal crest of trunk; sel_6, canal of nerve 6 of lateral electric field; *vrs*, ventro-lateral scales; *vs*, ventral scales.

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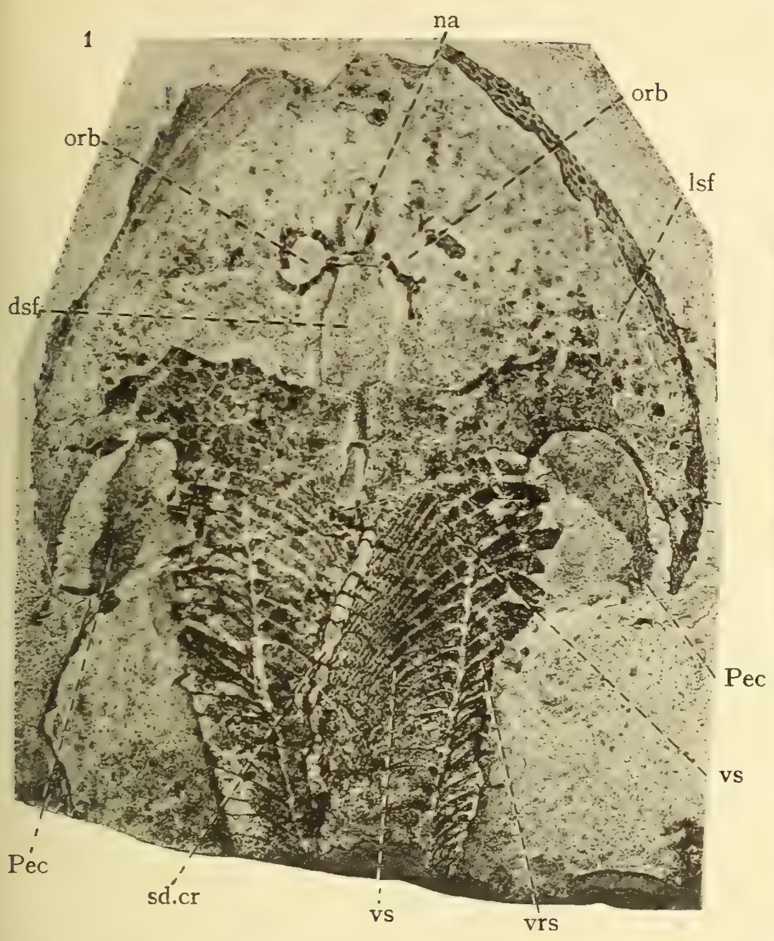

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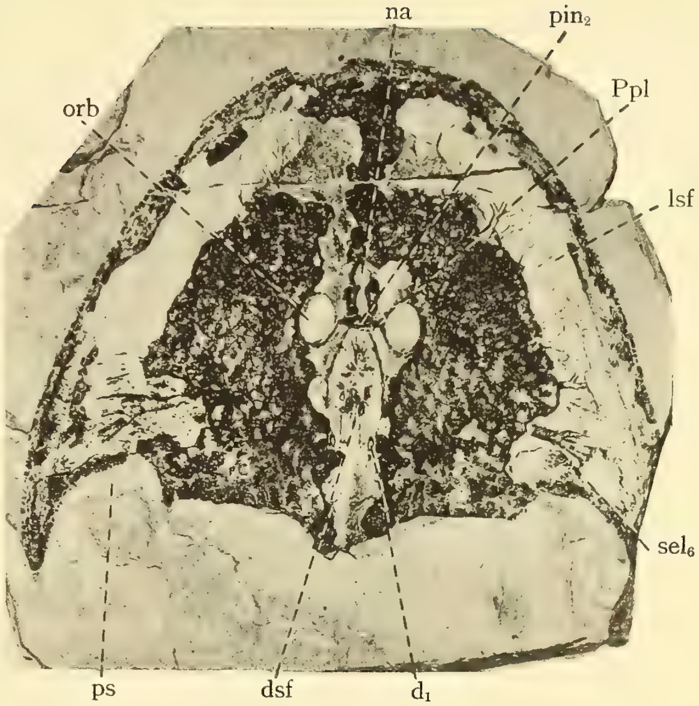

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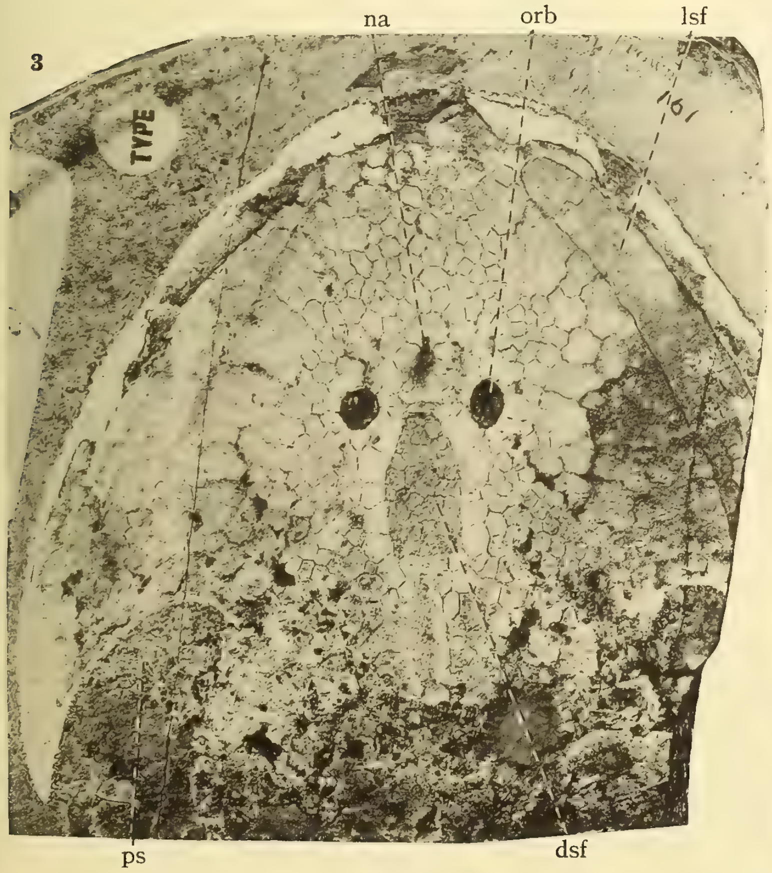

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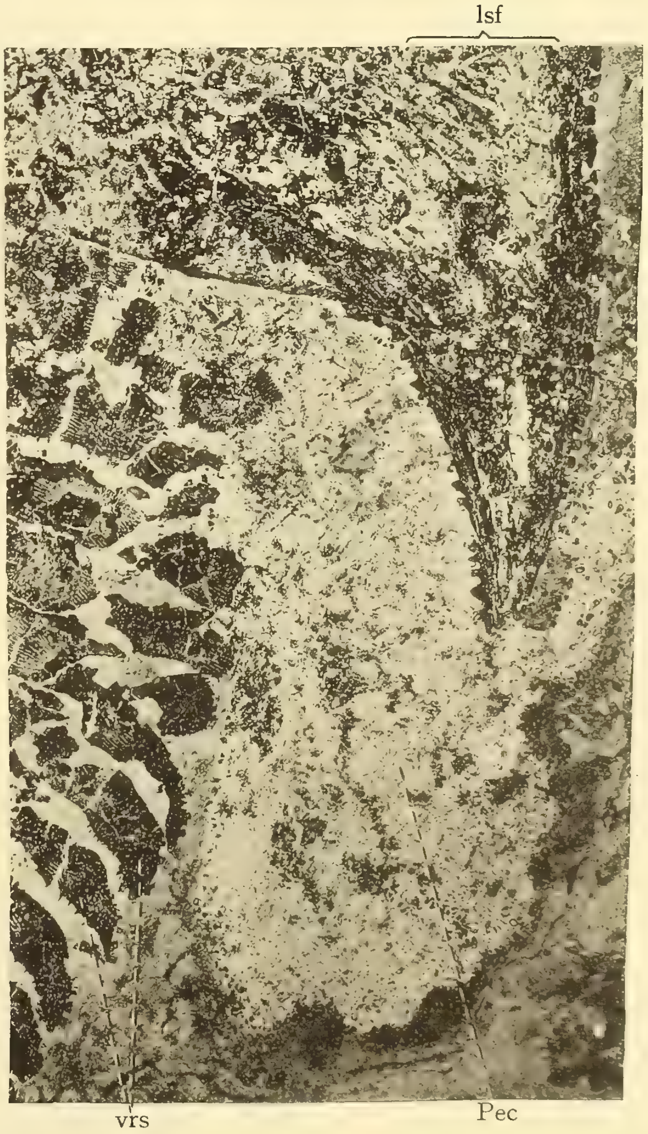

CEPHALASPIS

BRITISH
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NATURAL
HISTORY.

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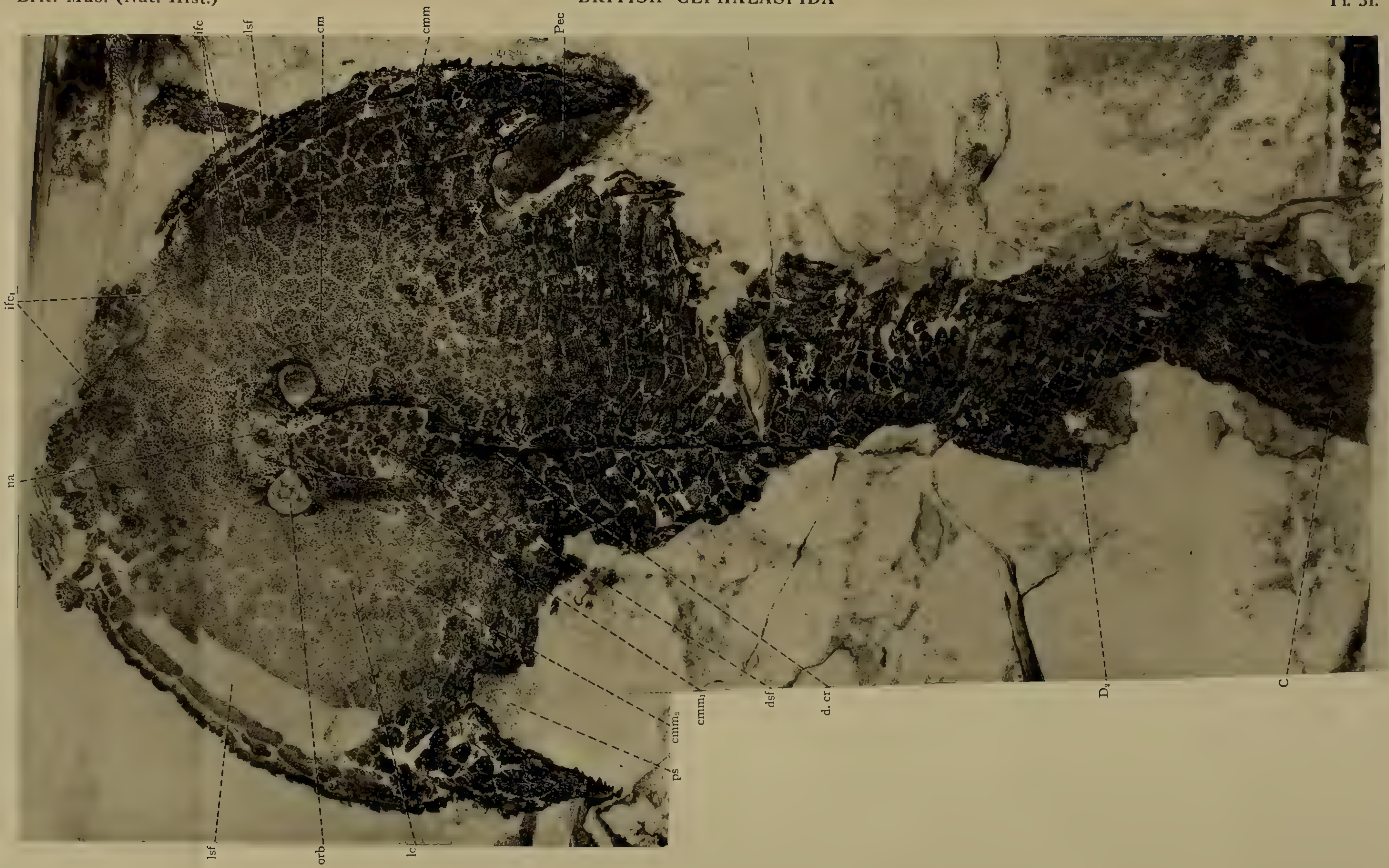
NATURAL HISTORY

PLATE 31.

Cephalaspis powriei Lankester, var. *asper* Lankester.

Almost complete specimen, probably of this variety. The cephalic shield is for the most part represented only by the most superficial parts of the dorsal exoskeleton, which are seen from the inner side. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.167.**—J. Powrie Coll.]. × 2½ diam.

C, caudal fin; *cm*, groove probably corresponding to pre-opercular or jugal canal of fishes; *cmm*, groove probably corresponding to middle head-line of pit-organs of fishes; cmm_1, cmm_2, groove corresponding either to posterior head-line of pit-organs or to supra-temporal cross-commissure of fishes; D_2, dorsal fin; *d.cr*, dorsal crest; *dsf*, dorsal electric field; *ifc*, infra-orbital groove; ifc_1, anterior division of infra-orbital groove, probably corresponding to supra-orbital sensory canal of fishes; *lc*, cephalic division of main lateral line; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbital opening; *Pec*, pectoral fin; *ps*, pectoral sinus.



CEPHALASPIS

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PLATE 32.

Cephalaspis salweyi Egerton.

FIG. 1.—Part of dorsal exoskeleton of cephalic shield, dorsal view. This area is bordering on the inner side of the posterior half of the left lateral electric field, and shows well the ornamentation and its relations to the polygonal areas. On the right side of the figure the tubercles have split off. Lower Old Red Sandstone : loc. unknown. British Museum [no. **42138.**—T. Baugh Coll., 1870]. × 3 diam.

Cephalaspis powriei Lankester, forma typica.

FIGS. 2, 3.—Dorsal exoskeleton of cornua made transparent by means of xylol, ventral view. (Same specimen as in Pl. 27, fig. 2.) × 3 diam.

FIG. 4.—Part of mucous canal system of dorsal exoskeleton of cephalic shield, basal (inner) view. The exoskeleton was made transparent by means of xylol. (Same specimen as in figs. 2, 3 and Pl. 27, fig. 2.) × 17 diam.

Cephalaspis pagei Lankester.

FIG. 5.—Small cephalic shield, dorsal view. Medially and posteriorly on the left side part of the oralo-branchial chamber is shown as an impression. Lower Old Red Sandstone : Pitairlie Quarry, Forfarshire. British Museum [no. **P. 16149.**—*ex* Coll. Dundee Museum, 1932]. Nat. size.

Cephalaspis whitei, sp. nov.

FIG. 6.—Part of left cornu, dorsal view. (Same specimen, the HOLOTYPE, as in text-fig. 9; Pl. 20, fig. 3; and Pl. 21.) × 4 diam.

bc, external branches from radiating canals (they are seen ascending between the meshes of the mucous canals just previous to passing into dentine canals) ; *iac,* inter-areal mucous canals (in fig. 1 grooves) ; *ita,* intra-areal mucous canals ; *k,* impression of branchial fossae ; *lsf,* lateral electric field ; *pr.orb,* impression of orbital prominence on roof of oralo-branchial chamber ; *ps,* pectoral sinus ; *rad.c,* radiating canals.

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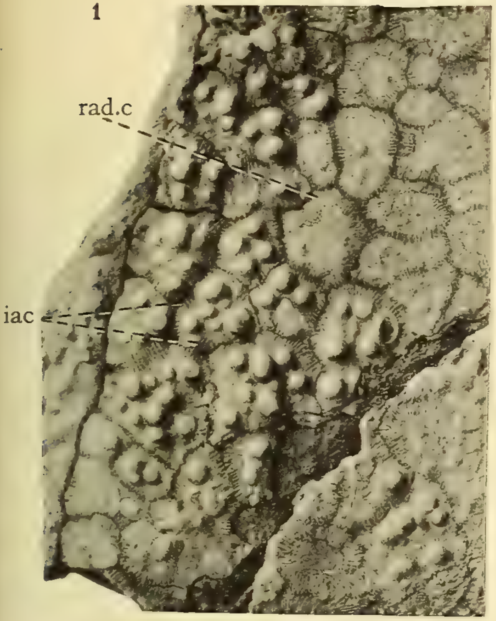

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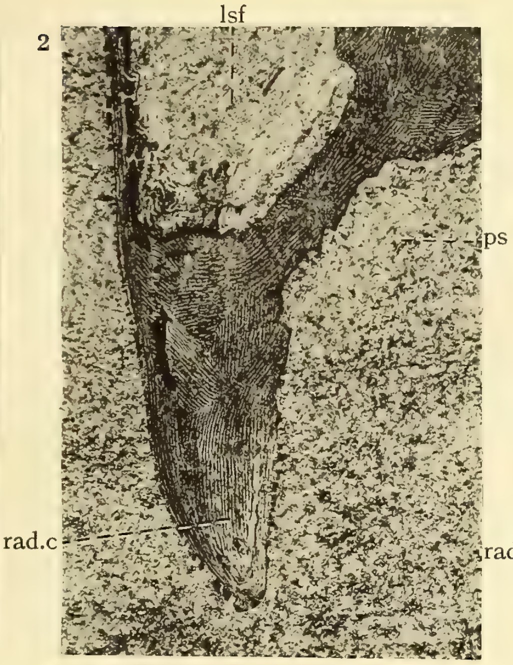

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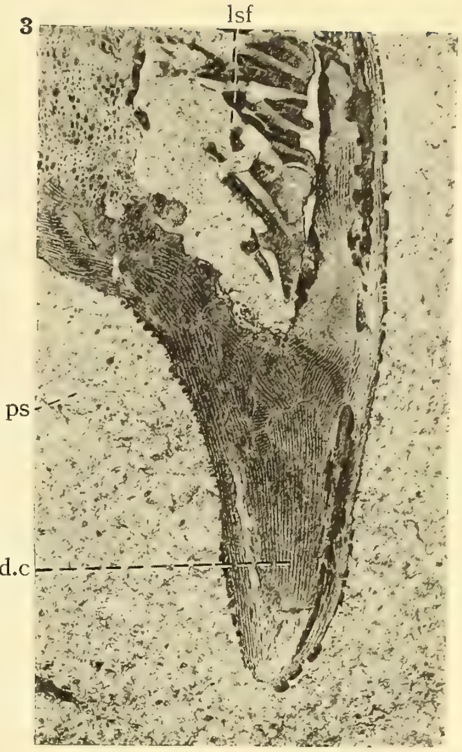

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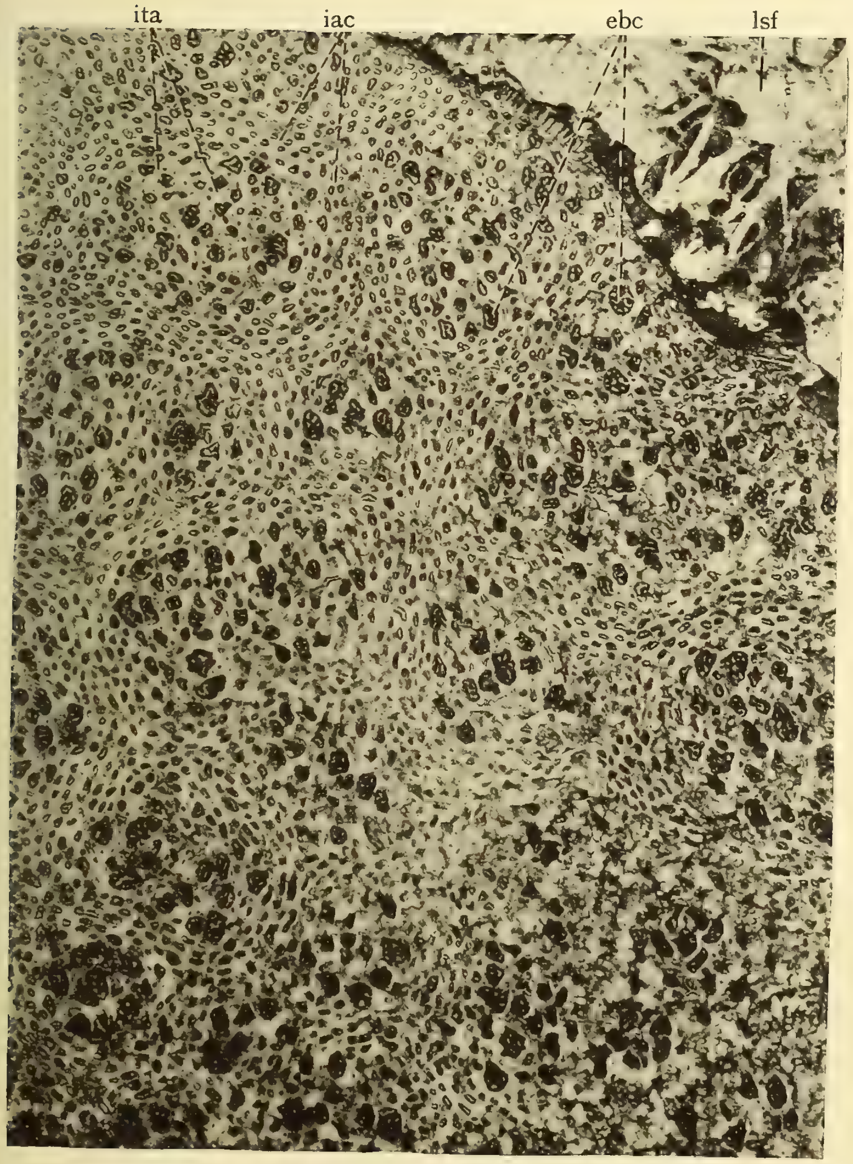

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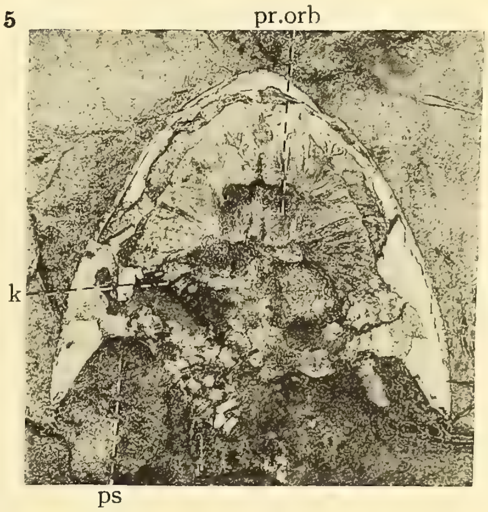

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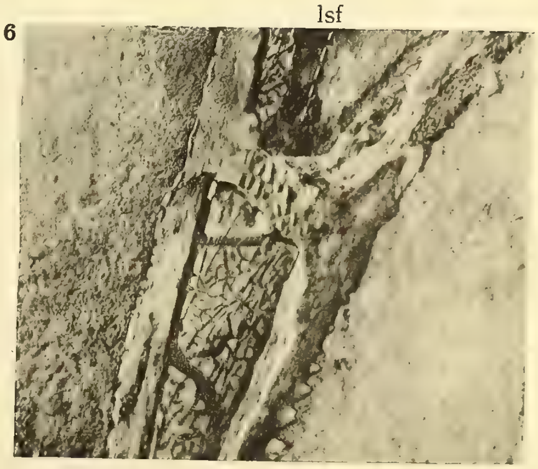

CEPHALASPIS

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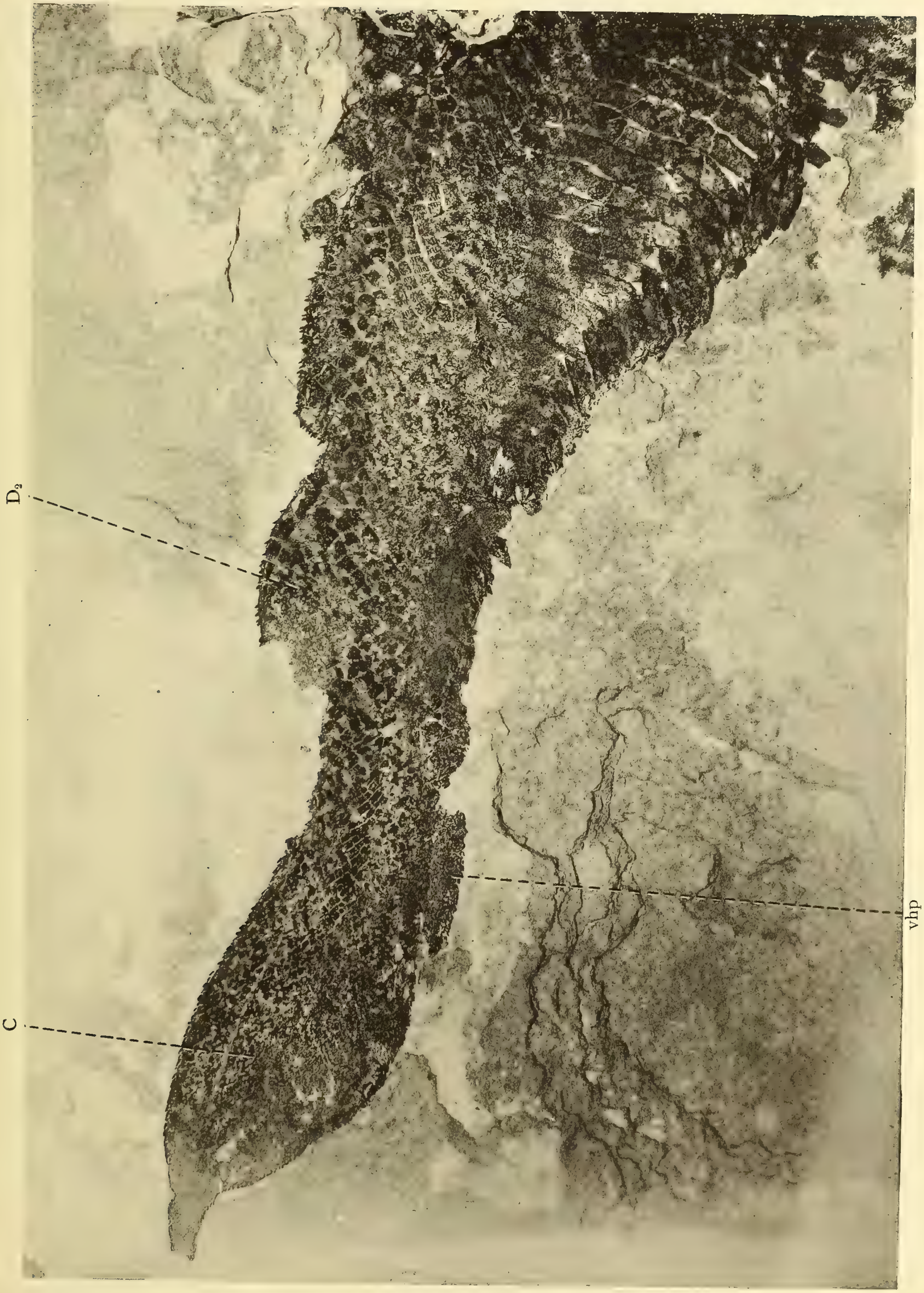
PLATE 33.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

Caudal region of laterally compressed specimen. Both the dorsal and caudal fins are well displayed. Lower Old Red Sandstone: Turin Hill, Forfarshire. British Museum [no. **P. 670.**—P. M. G. Egerton Coll., 1882]. × 2½ diam.

C, caudal fin; D_2, dorsal fin; *vhp*, ventral axis of caudal fin with membrane.



CEPHALASPIS

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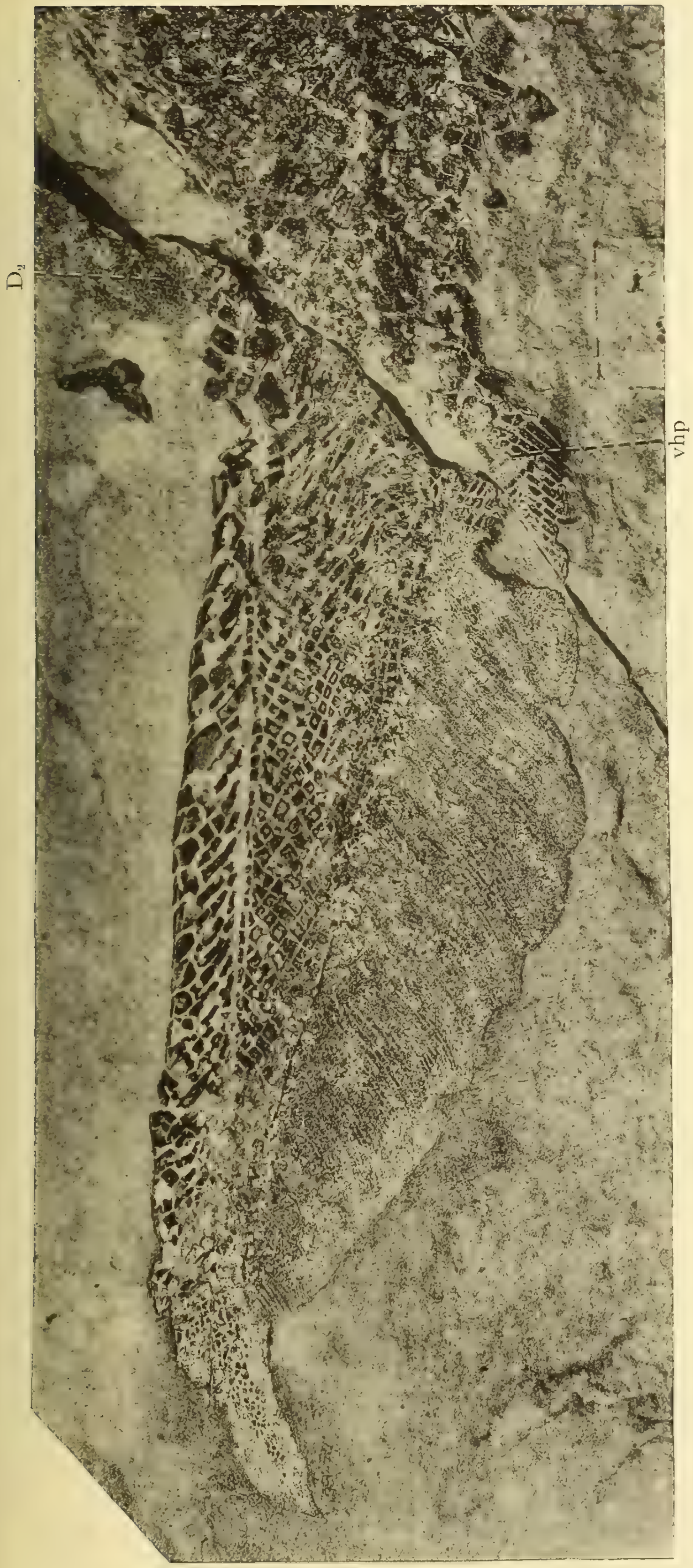
NATURAL HISTORY

PLATE 34.

Cephalaspis sp.

FIGS. 1, 2.—Caudal fin in counterpart, lateral view. Lower Old Red Sandstone: Turin Hill, Forfarshire. (Fig. 1) Royal Scottish Museum, Edinburgh [no. **1891.92.172.**—J. Powrie Coll.]. (Fig. 2) British Museum [no. **P. 16147.**—Kinnaird Coll., *ex* Coll. Dundee Museum, 1932]. × 3 diam.

D_2, dorsal fin (fragments only); *vhp*, ventral axis of caudal fin with membrane.



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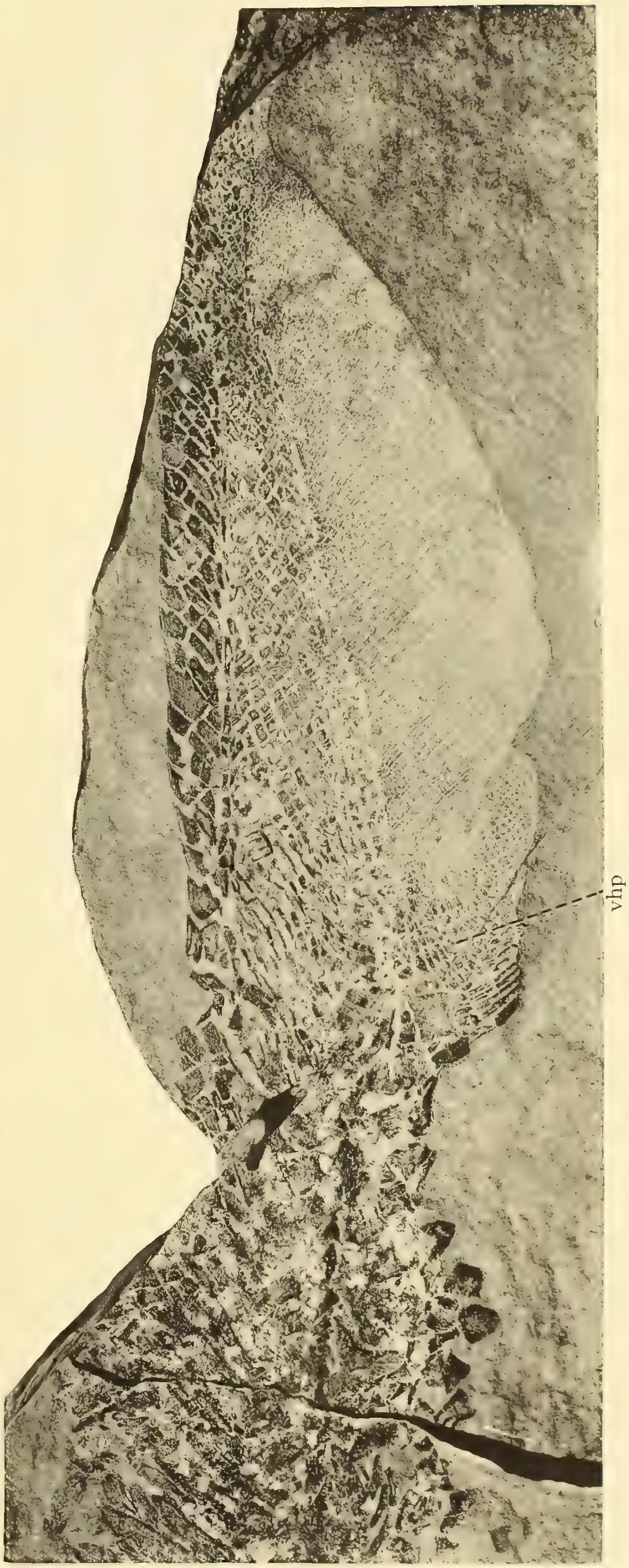

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CEPHALASPIS

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PLATE 35.

Cephalaspis lornensis Traquair.

Fig. 1.—Cephalic shield, dorsal view. Over most of this specimen only the most proximal parts of the basal layer of the dorsal exoskeleton are preserved. Lower Old Red Sandstone *: Oban, Argyllshire. Royal Scottish Museum, Edinburgh [no. **1901.68.27**]. × 2 diam.

Fig. 2.—Cephalic shield, dorsal view. The dorsal exoskeleton is very imperfectly preserved. Lower Old Red Sandstone *: Oban, Argyllshire. British Museum [no. **P. 9642.**—Geol. Surv. Scotland, 1901]. × 2 diam.

Cephalaspis pagei Lankester.

Fig. 3.—Exoskeleton of left side of almost complete specimen. The greater part of this specimen shows the basal (inner) surface. Lower Old Red Sandstone: loc. uncertain, Forfarshire. British Museum [no. **P. 492.**—P. M. G. Egerton Coll., 1882]. × 2 diam.

D_2, dorsal fin; d_2, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *d.cr*, dorsal crest of trunk; *dsf*, dorsal electric field; *d.sp*, dorsal spine of cephalic shield; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *otl*, posterior margin of endoskeleton of otic region, continuous laterally with medial margin of endoskeletal shoulder-girdle, medially with lateral margin of endoskeleton of occipital region; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; sel_1–sel_6, canals of electric nerves 1–6 of lateral electric field.

* See p. 201.

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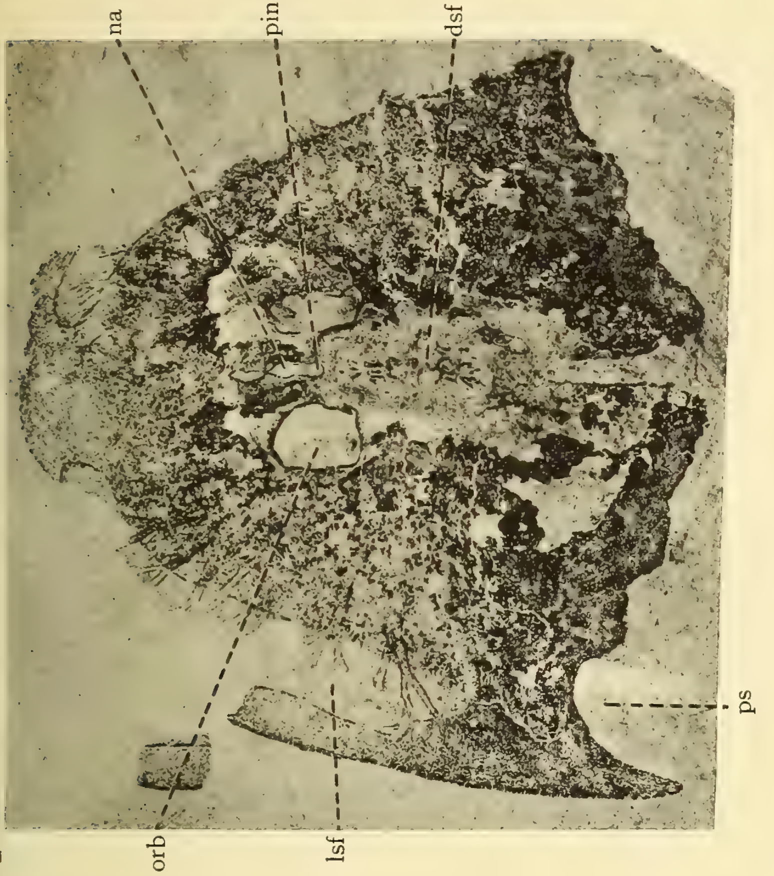

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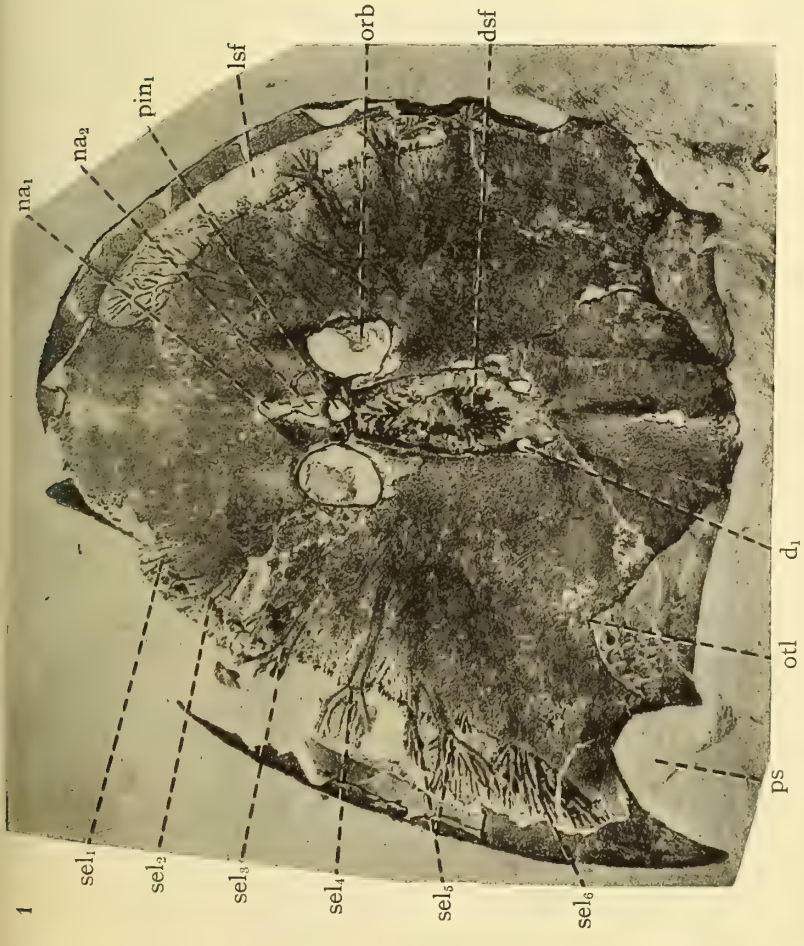

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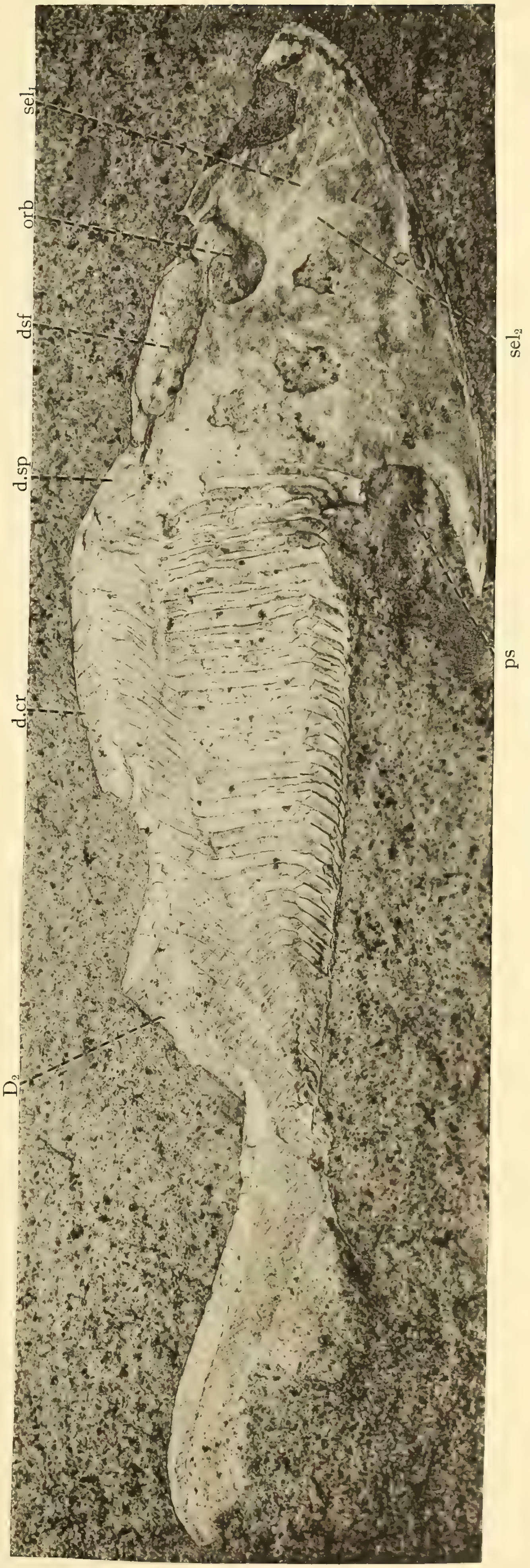

CEPHALASPIS

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NATURAL
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PLATE 36.

Cephalaspis salweyi Egerton.

Fig. 1.—Casts of venous ring-sinuses. The exoskeleton has been removed to show the casts. (Same specimen as in Pl. 11, fig. 3—**P. 190**.) × 3 diam.

Fig. 2.—Grooves for venous ring-sinuses on inner surface of basal layer of exoskeleton. (Counterpart of specimen in fig. 1—see also Pl. 11, fig. 3—**P. 188.**) × 3 diam.

Cephalaspis pagei Lankester.

Fig. 3.—Dorsal exoskeleton of cephalic shield and anterior part of squamation, ventral (inner) view. Lower Old Red Sandstone: loc. unknown. Royal Scottish Museum, Edinburgh [no. **1932–17**]. × 3 diam.

Fig. 4.—Part of cephalic shield of same specimen further magnified to show development of mucous canal system. Where the surface has a reticular appearance, only the superficial layer with the pores of the mucous canal system has been preserved; where the mucous canals and the radiating canals are to be seen, parts of the middle layer are also present. Basal (inner) view. Approx. × 12 diam.

Fig. 5.—Dorsal exoskeleton of cephalic shield, ventral (inner) view. The exoskeleton is very imperfectly preserved. Lower Old Red Sandstone: loc. uncertain, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1886.31.18**]. × 1½ diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals in basal layer of exoskeleton; *cm*, groove corresponding either to pre-opercular or jugal sensory canal of fishes; *dsf*, dorsal electric field; *ifc*, infra-orbital groove; *ifc*$_1$, anterior division of infra-orbital groove, probably corresponding to supra-orbital sensory canal of fishes; *lc*, groove representing the cephalic division of main lateral line of fishes; *ls*, lateral scales of trunk; *lsf*, lateral electric field; *mc*, mucous canals; *na*, naso-hypophysial aperture; *na*$_2$, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *ps*, pectoral sinus; *rad.c*, radiating canals in middle layer of exoskeleton; *r.sin*, venous ring-sinuses; *sl*, superficial layer of exoskeleton (its reticular appearance is caused by the numerous fine pores of the mucous canal system).

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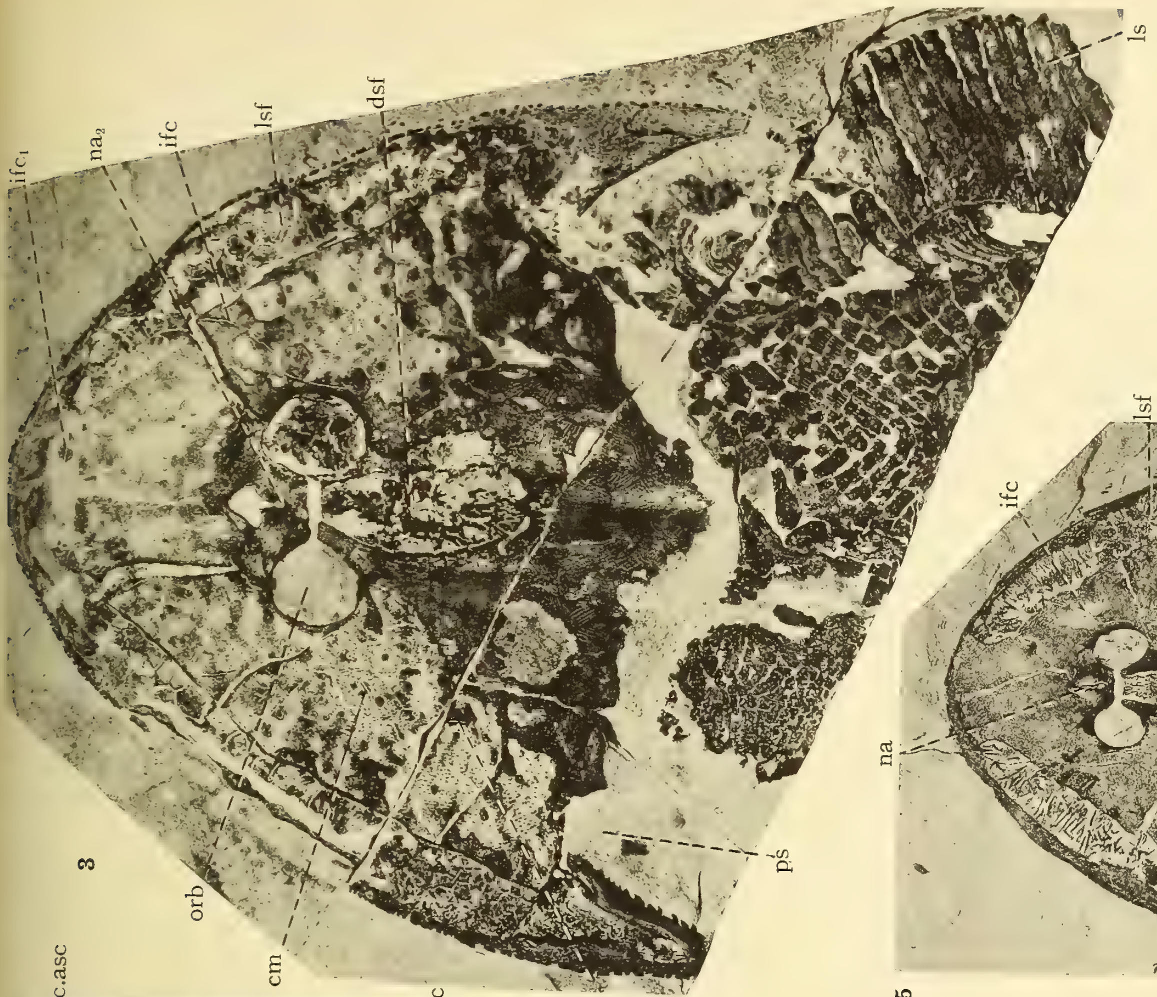

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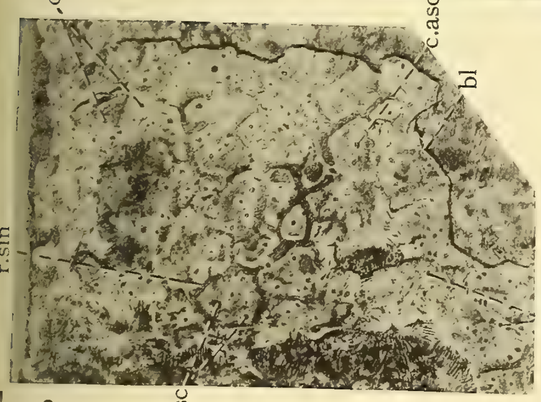

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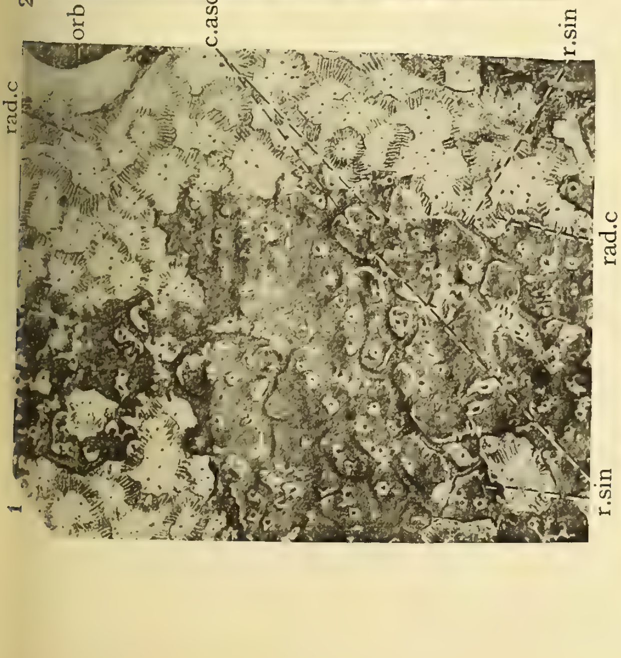

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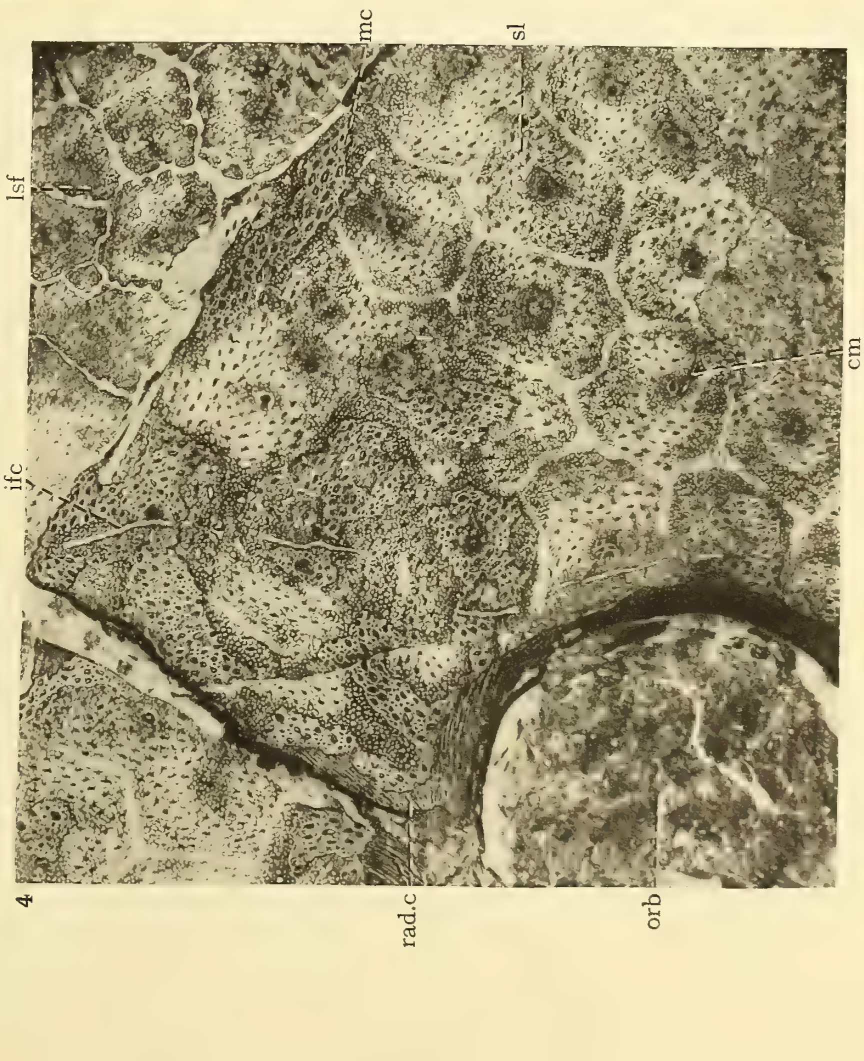

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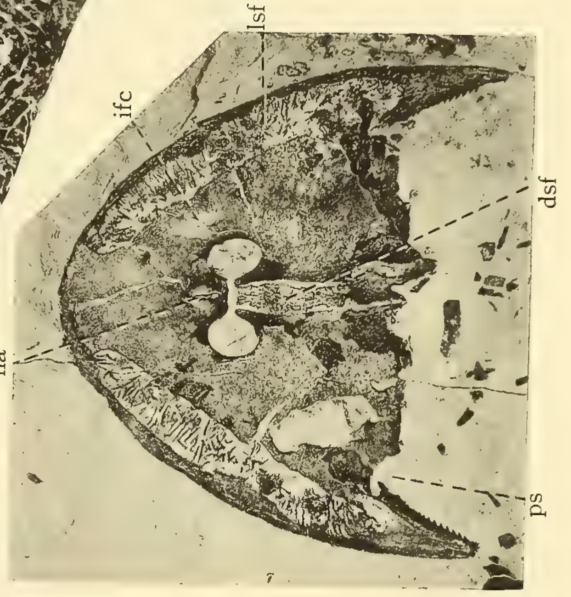

CEPHALASPIS

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NATURAL HISTORY

PLATE 37.

Cephalaspis spp.

FIG. 1.—Cephalic shield probably representing a new species, dorsal view. The dorsal exoskeleton of the shield is represented largely by the proximal parts of the basal layer only. Lower Old Red Sandstone: Glammis, Forfarshire. British Museum [no. **P. 3234.**—Enniskillen Coll., 1882]. Nat. size.

FIG. 2.—Part of squamation of trunk of either *C. pagei* Lank., or a variety of *C. powriei* Lank., preserved very largely as an impression of the outer side. Lower Old Red Sandstone: loc. uncertain, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.173.**—J. Powrie Coll.]. × 1½ diam.

Cephalaspis pagei Lankester.

FIG. 3.—Dorsal exoskeleton of cephalic shield with adjacent parts of squamation of trunk, ventral (inner) view. Lower Old Red Sandstone: near Reswallie, Forfarshire. Sedgwick Museum, Cambridge [no. **A. 3313.**—Mrs. G. F. Browne Coll.]. × 3 diam.

dpr, impression of supra-oral field; *dsf*, dorsal electric field; *ls*, lateral scales; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *Pec*, pectoral fin; pin_2, pineal opening in pineal plate; *Ppl*, pineal plate; *pr.orb*, impression of orbital prominence; *ps*, pectoral sinus; *r.aort*, impression of aortic ridge; *vrs*, ventro-lateral scales.

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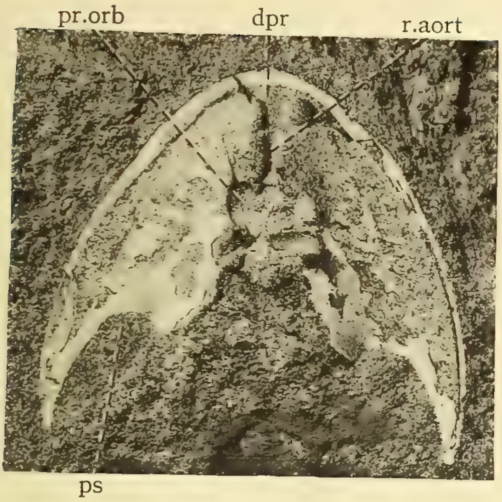

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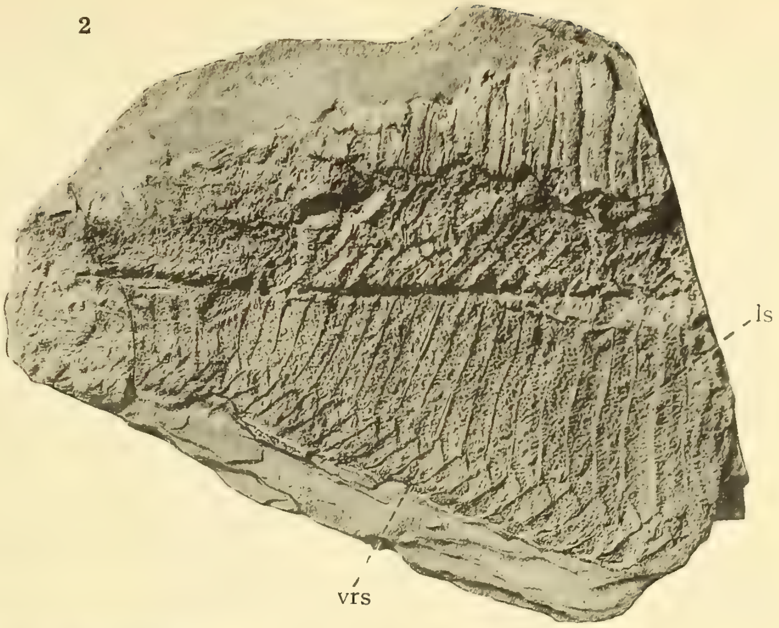

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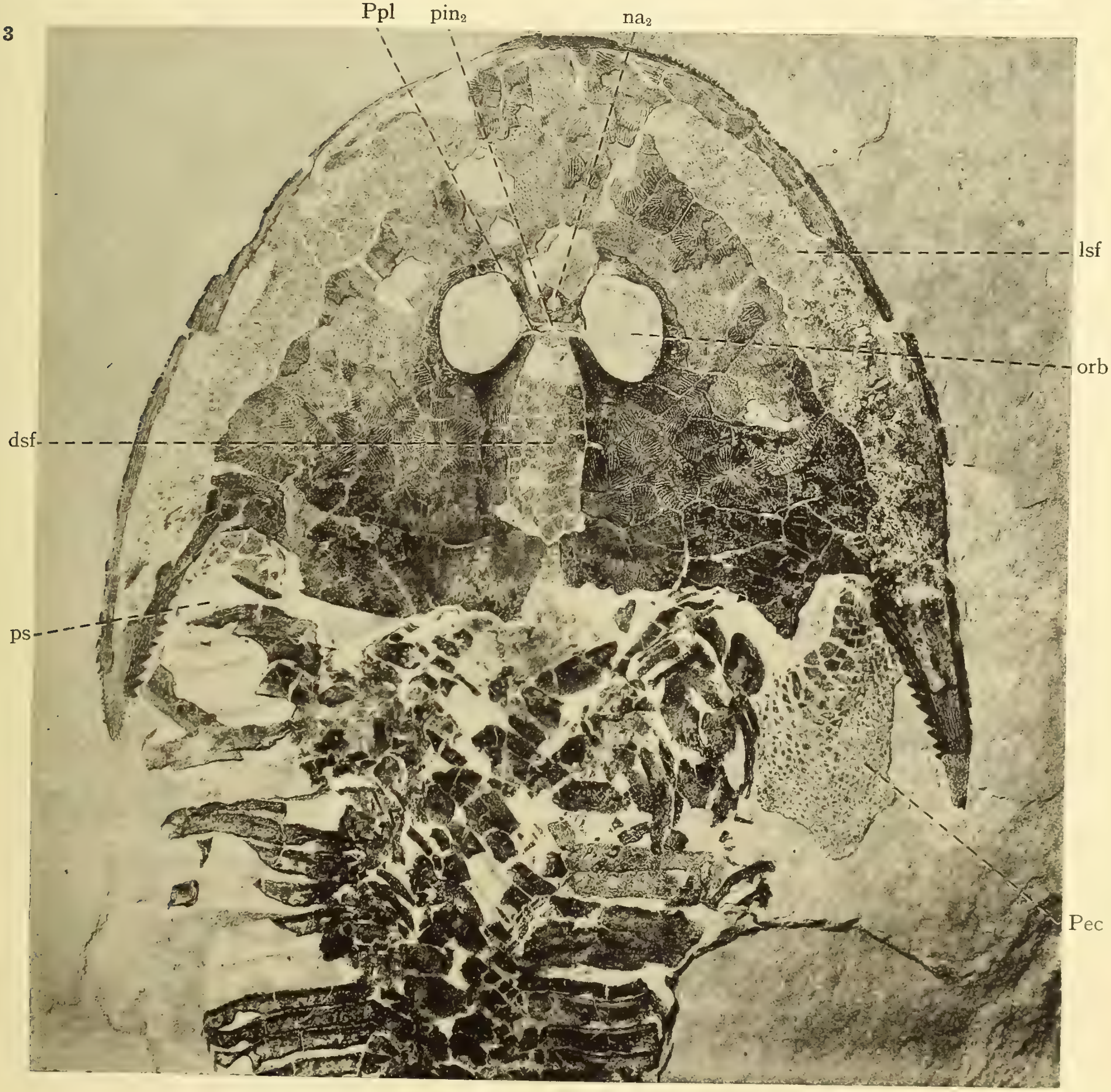

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PLATE 38.

Cephalaspis pagei Lankester.

FIG. 1.—Cephalic shield and part of squamation, dorsal view. Lower Old Red Sandstone: Turin Hill, Forfarshire. British Museum [no. **P. 124.**—Purchased, 1880]. × 2 diam.

FIG. 2.—Cephalic shield, dorsal view. The dorsal exoskeleton is preserved only in patches. Lower Old Red Sandstone: Tealing, Forfarshire. British Museum [no. **P. 6949.**—Hugh Mitchell Coll., 1893]. × 2 diam.

FIGS. 3, 4.—Specimen flattened dorso-ventrally, showing cephalic shield and considerable part of trunk, in counterpart. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.147.**—J. Powrie Coll.]. × 3 diam.

D_2, dorsal fin; *dsf*, dorsal electric field; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *orb*, orbit or orbital opening; pin_1, pineal opening on dorsal side of endocranial part of cephalic shield; *ps*, pectoral sinus; *sclr*, sclerotic ring; sel_1–sel_4, canals of nerves 1–4 of lateral electric field; $v.ls_3$, canal of dorso-lateral superficial vein 3.

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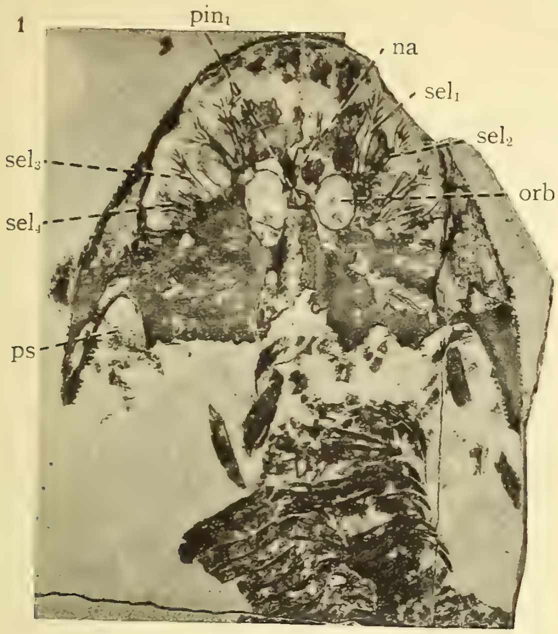

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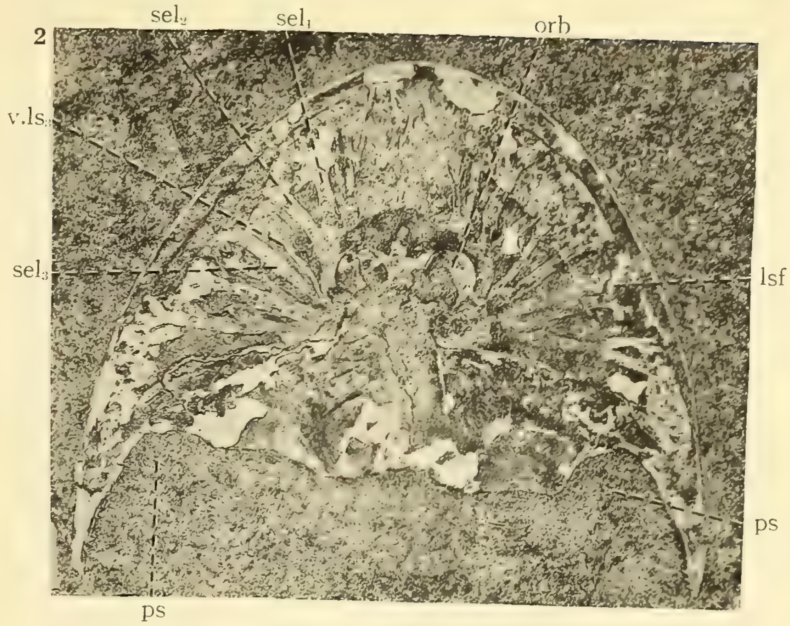

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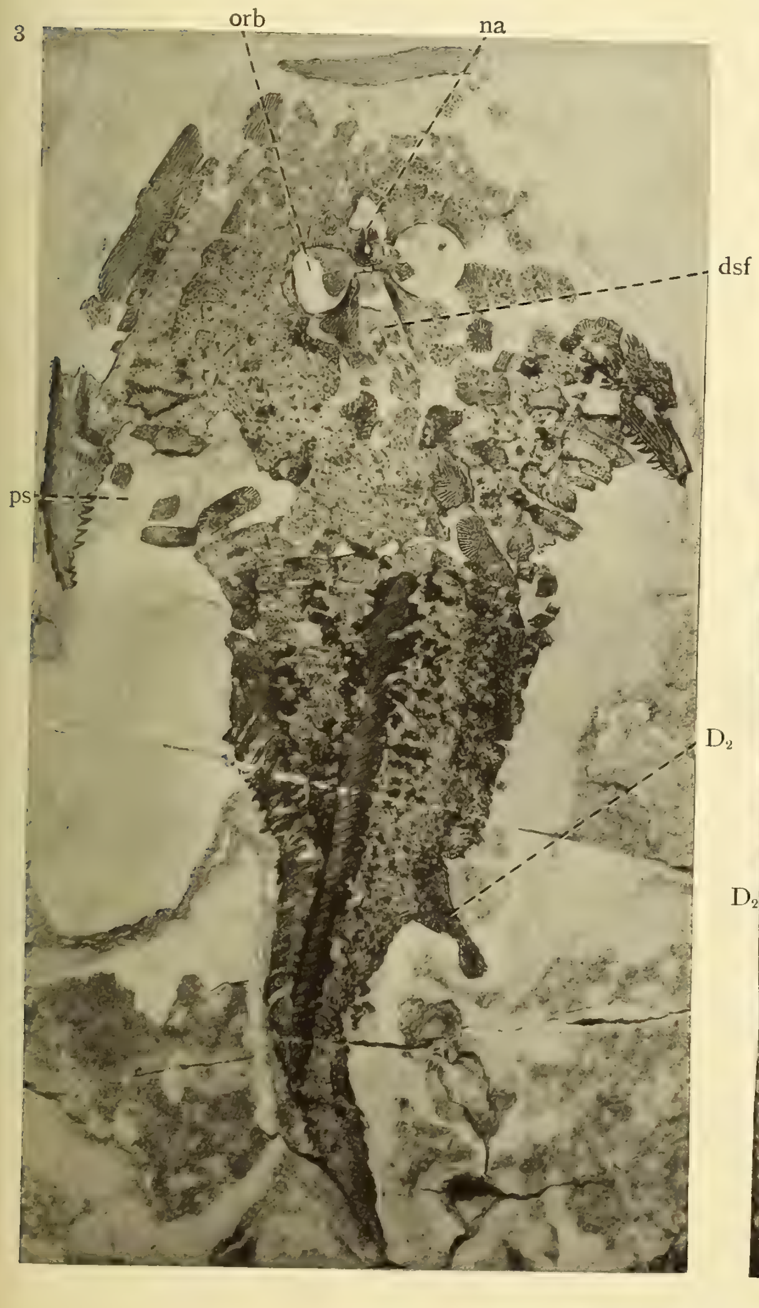

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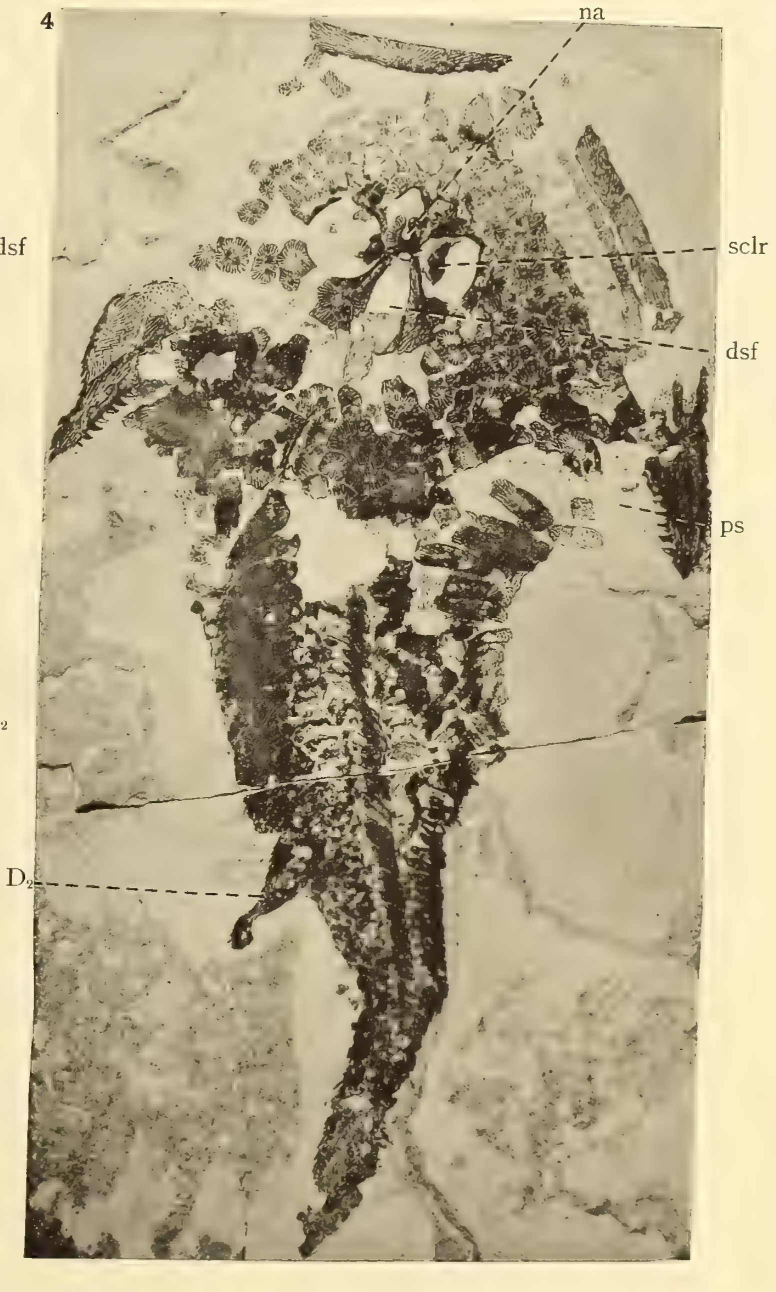

CEPHALASPIS

PLATE 39.

Cephalaspis pagei Lankester.

FIG. 1.—Fairly complete but much-flattened specimen. The cephalic shield is in dorsal view, but the scales of the trunk are preserved mainly as impressions of their external surfaces. Lower Old Red Sandstone: Turin Hill, Forfarshire. LECTOTYPE. Royal Scottish Museum, Edinburgh [no. **1891.92.148.**—J. Powrie Coll.]. × 2½ diam.

FIG. 2.—A similar specimen. The cephalic shield is in dorsal view; the squamation is represented mainly by the scales of the left half of the trunk, which are exposed from the medial (inner) side. Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.153.**—J. Powrie Coll.]. × 3 diam.

C, caudal fin; D_2, dorsal fin; *dsf*, dorsal electric field; *ls*, lateral scales; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *ps*, pectoral sinus; *sclr*, sclerotic ring; *vrs*, ventro-lateral scales.

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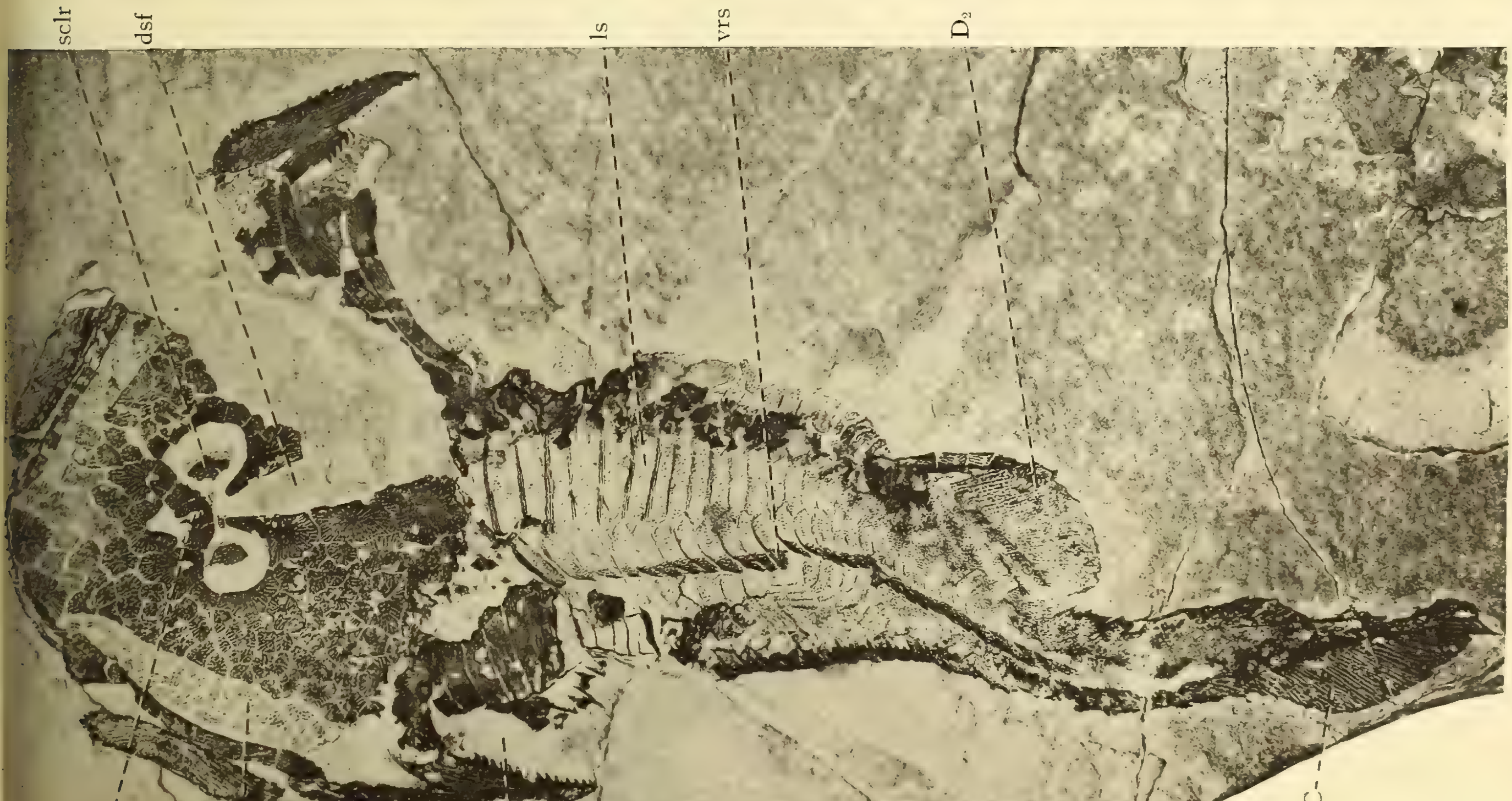

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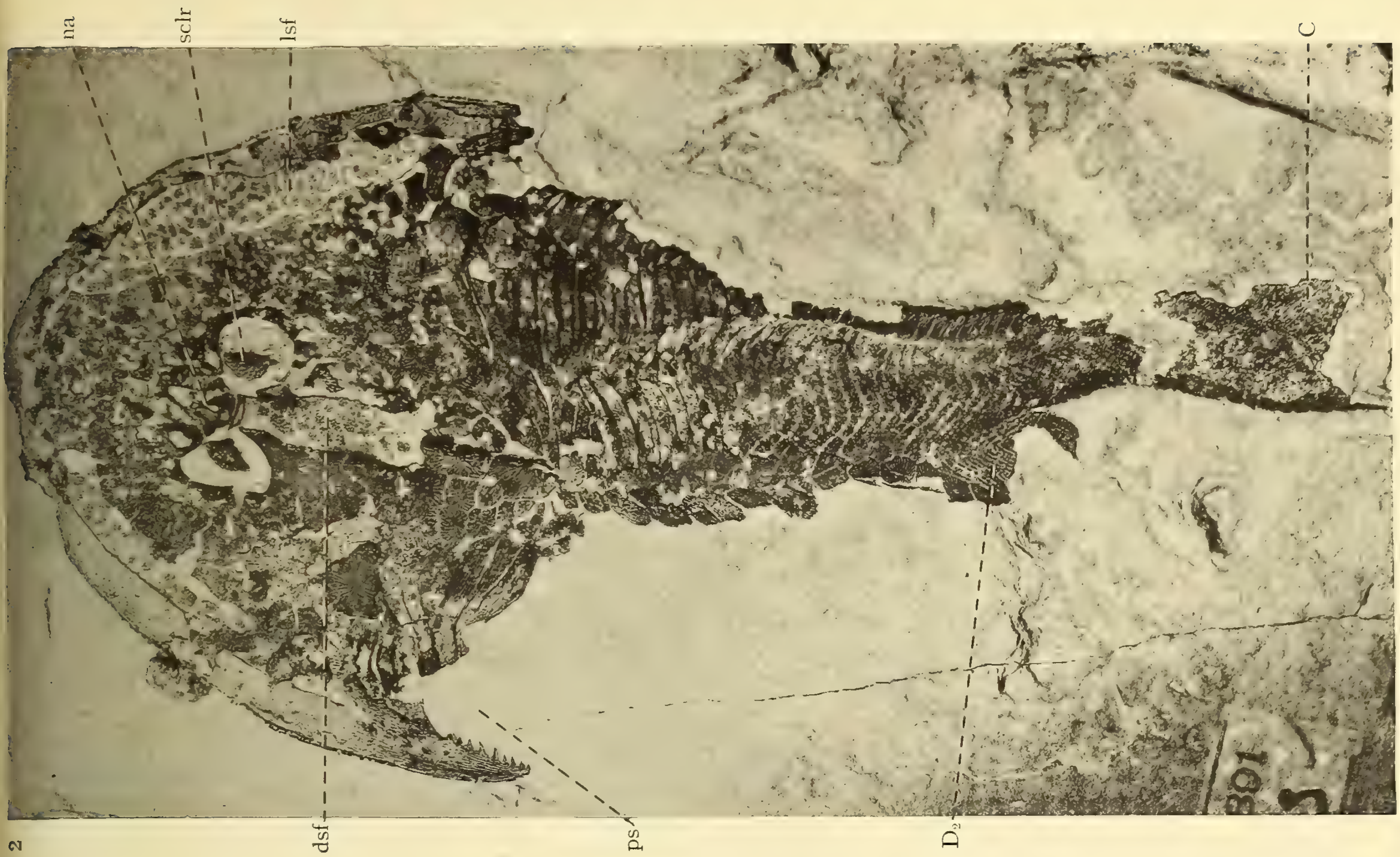

CEPHALASPIS

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PLATE 40.

Cephalaspis pagei Lankester.

Fig. 1.—Much-flattened specimen. The dorsal exoskeleton of the cephalic shield and the squamation are largely represented by external impressions. (See also Pl. 42, fig. 1.) Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.156.**—J. Powrie Coll.]. × 2½ diam.

Thyestes egertoni (Lankester).

Fig. 2.—Specimen lacking caudal region, dorsal view. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 6023(IV).**—G. H. Piper Coll., 1889]. × 3 diam.

Cephalaspis acutirostris, sp. nov.

Fig. 3.—Cephalic shield with part of squamation, ventral view. Lower Old Red Sandstone: near Ludlow,* Shropshire. Holotype. British Museum [no. **P. 9763.**—G. H. Morton Coll., 1900 (Colld. A. Marston, 1860)]. × 2 diam.

C, caudal fin; cmm_1, groove corresponding to either posterior head-line of pit-organs or supra-temporal cross-commissure of fishes; d_1, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *dsf,* dorsal electric field; *f.cn,* fossa circum-nasalis; *ifc,* infra-orbital sensory canal groove; ifc_1, anterior division of infra-orbital groove, probably corresponding to supra-orbital sensory canal of fishes; *ls,* lateral scales; *lsf,* lateral electric field; *orb,* orbital opening; *p.a,* pectoral angle of cornu; *Pec,* pectoral fin; pin_1, pineal opening on dorsal side of endo-skeleton of cephalic shield; *ps,* pectoral sinus; *ra,* rostral process (imperfect anteriorly); *rs,* dorsal ridge-scales; *vrs,* ventro-lateral scales; *vs,* ventral scales.

* See p. 200.

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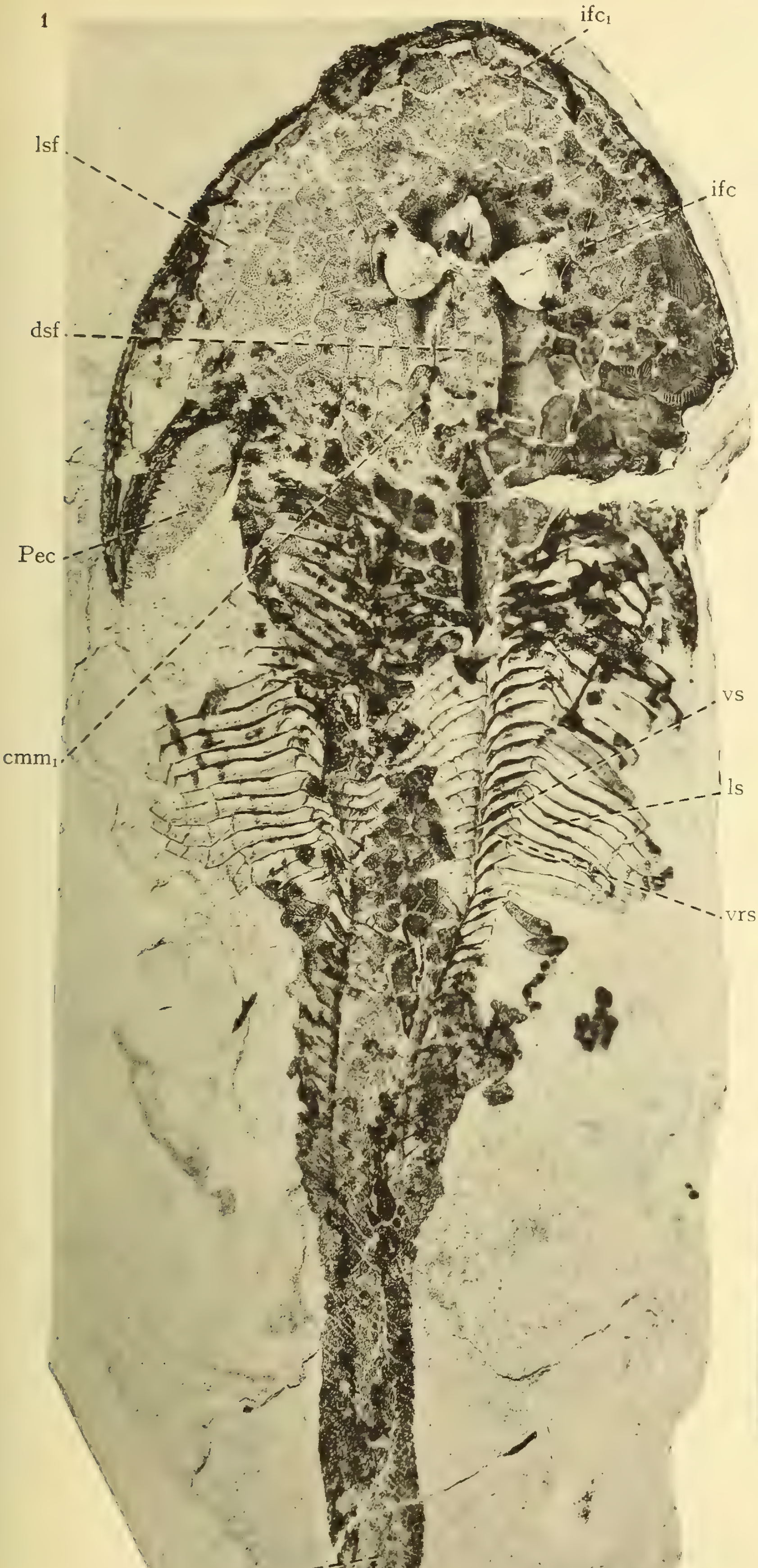

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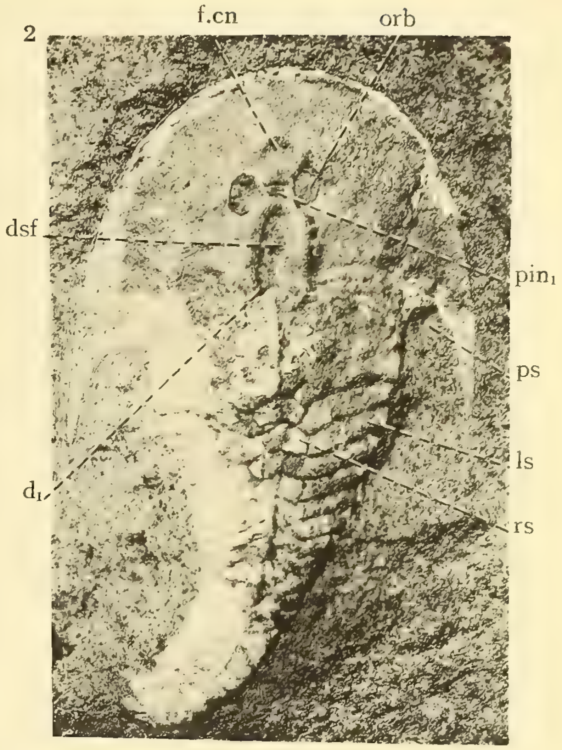

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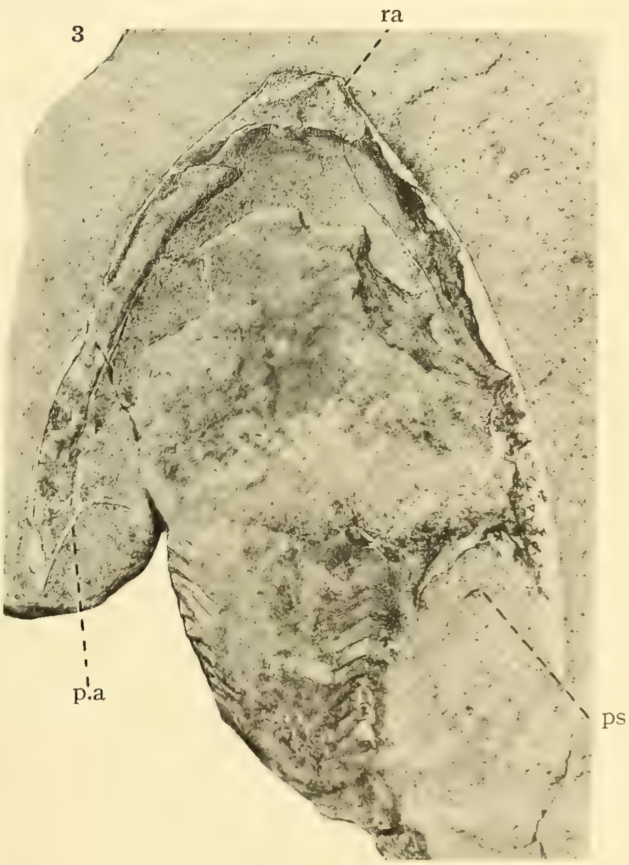

CEPHALASPIS and THYESTES

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PLATE 41.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

Fig. 1.—Part of dorsal exoskeleton of cephalic shield doubtfully referred to this form, basal view. The specimen has been made transparent by means of xylol in order to show the arrangement of the vascular canals in the basal layer and the neighbouring parts of the middle layer. (Same specimen as in Pl. 22, fig. 7.) Approx. × 15 diam.

Cephalaspis powriei Lankester, forma typica.

Fig. 2.—Part of dorsal exoskeleton of cephalic shield doubtfully referred to this form, dorsal view. The specimen has been made transparent by means of xylol in order to show the disposition and course of some of the vascular canals. (Same specimen as in Pl. 26, fig. 2.) Approx. × 15 diam.

c.asc, ascending vascular canals; *c.des*, descending vascular canals; *rad.c*, radiating canals; *r.sin*, venous ring-sinuses more or less imperfectly developed in interior of basal layer.

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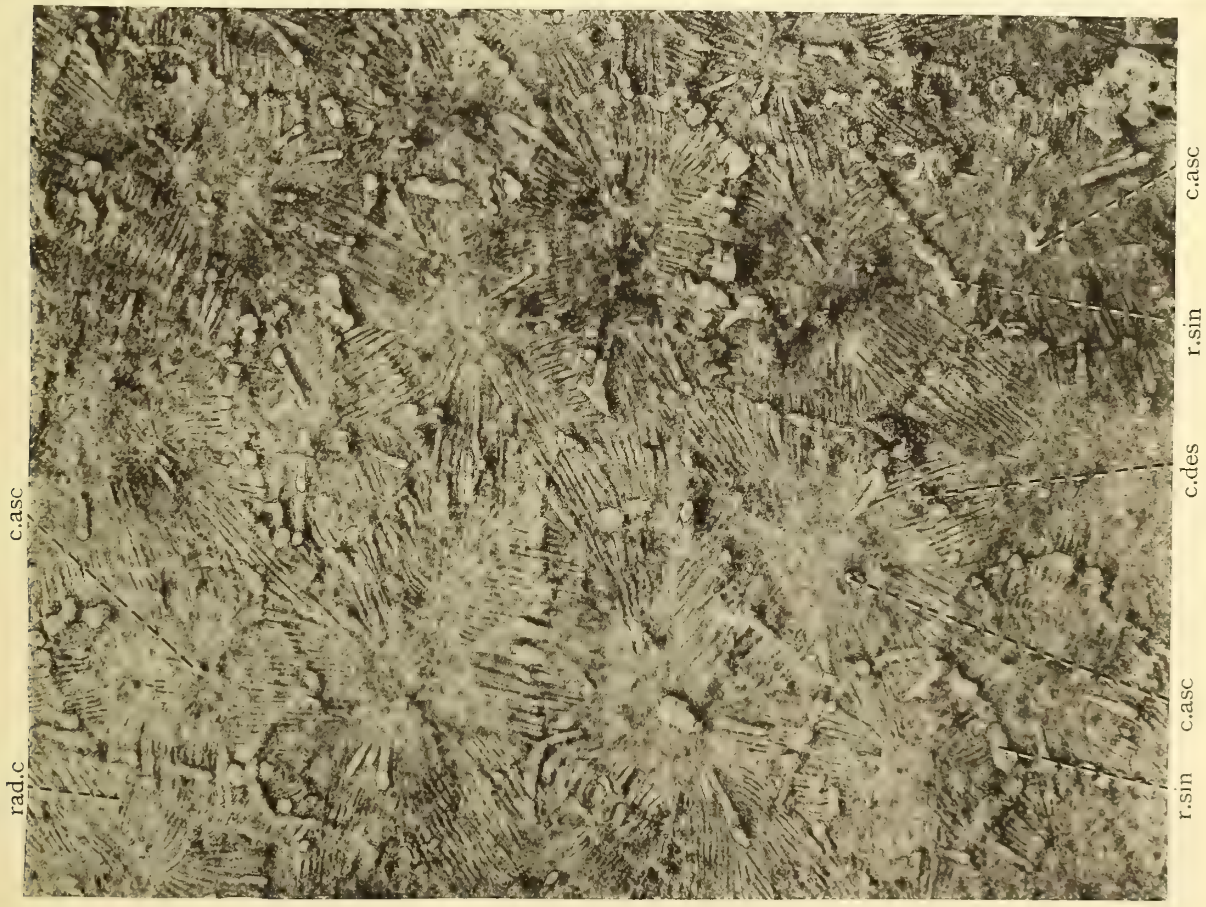

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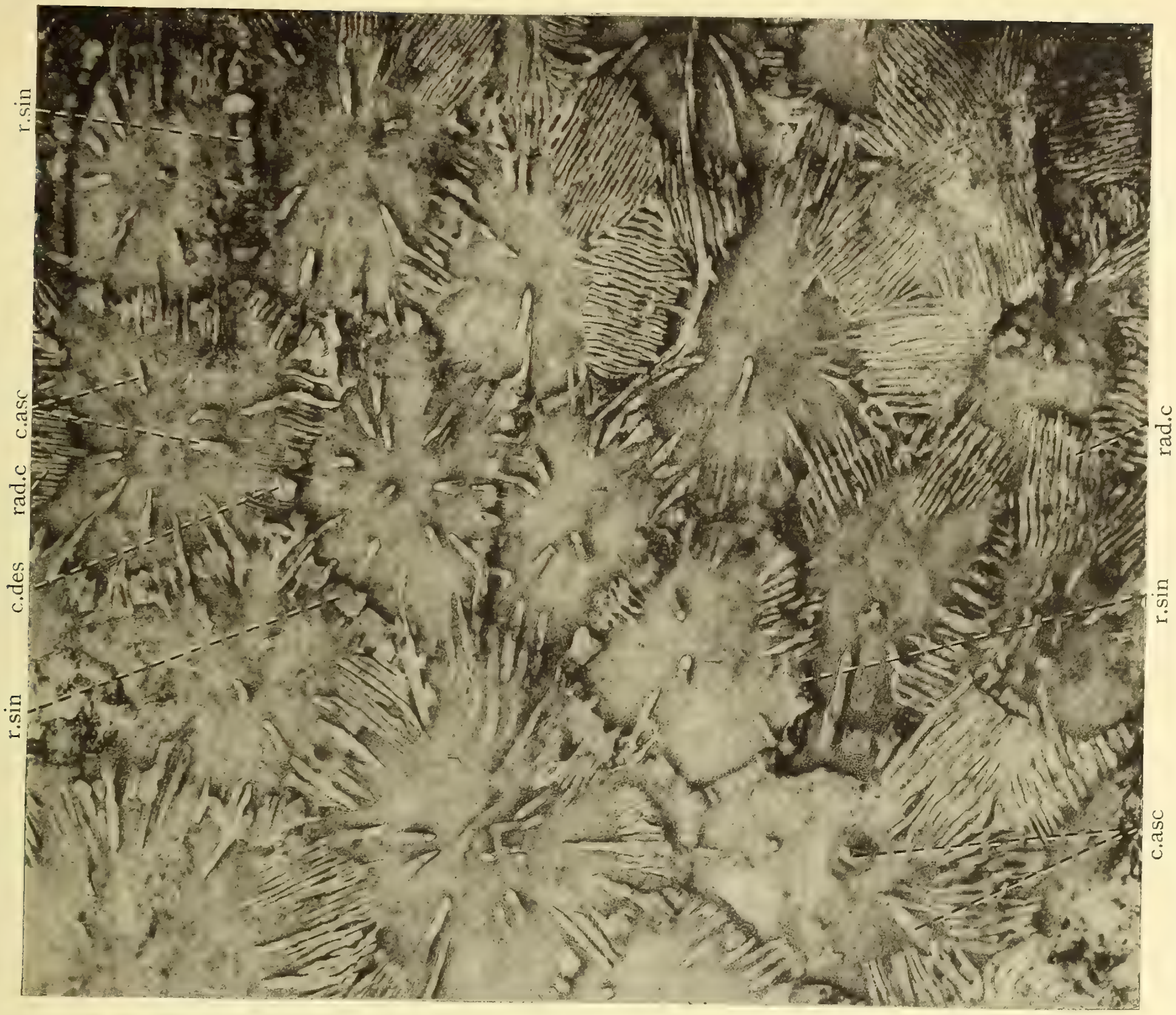

CEPHALASPIS

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PLATE 42.

Cephalaspis pagei Lankester.

FIG. 1.—Part of dorsal exoskeleton of cephalic shield close to orbital opening. The exoskeleton is to a great extent represented either by an impression of the external surface or by the most superficial parts. At (*a*) the superficial layer formed a continuous covering to the middle layer; but at (*b*) the superficial layer was absent, so that the mucous canal system was in the form of open grooves. (Same specimen as in Pl. 40, fig. 1.) Approx. × 15 diam.

FIG. 2.—Part of dorsal exoskeleton of cephalic shield preserved mainly as an impression of the external surface. The black spots in the centre of some of the polygonal areas are patches of the superficial layer which otherwise occurs only in the isolated tubercles of the ornament. The mucous canal system is in the form of open grooves. Lower Old Red Sandstone : Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.157.**—J. Powrie Coll.]. Approx. × 15 diam.

a, central parts of polygonal areas covered by superficial layer, mucous canal system consisting there of completely closed canals (fig. 1) ; *b*, peripheral parts of polygonal areas characterised by presence of superficial layer in isolated tubercles only (here the mucous canals are represented by open grooves) ; *cm*, sensory canal probably corresponding either to pre-opercular or jugal sensory canal of fishes ; *cmm*, sensory canal groove representing middle head-line of pit-organs of fishes ; *iac*, inter-areal mucous grooves ; *ifc*, infra-orbital sensory canal groove ; *ita*, intra-areal mucous grooves ; ita_1, closed intra-areal mucous canals ; *orb*, orbital opening ; *sclr*, sclerotic plate preserved as impression of ornamented dorsal side ; *sl*, superficial layer, its reticular appearance caused by numerous pores of mucous canals which lay beneath it.

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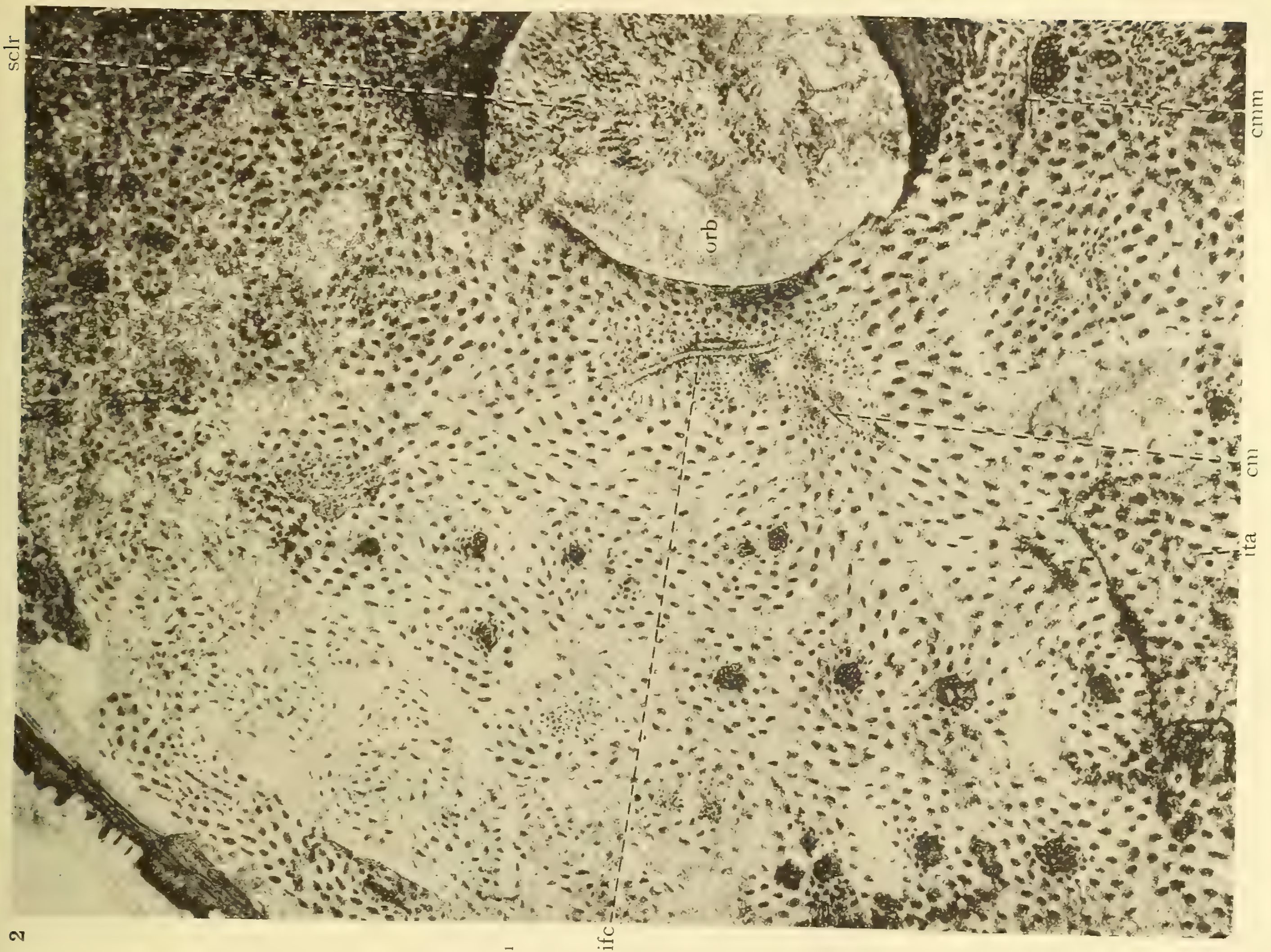

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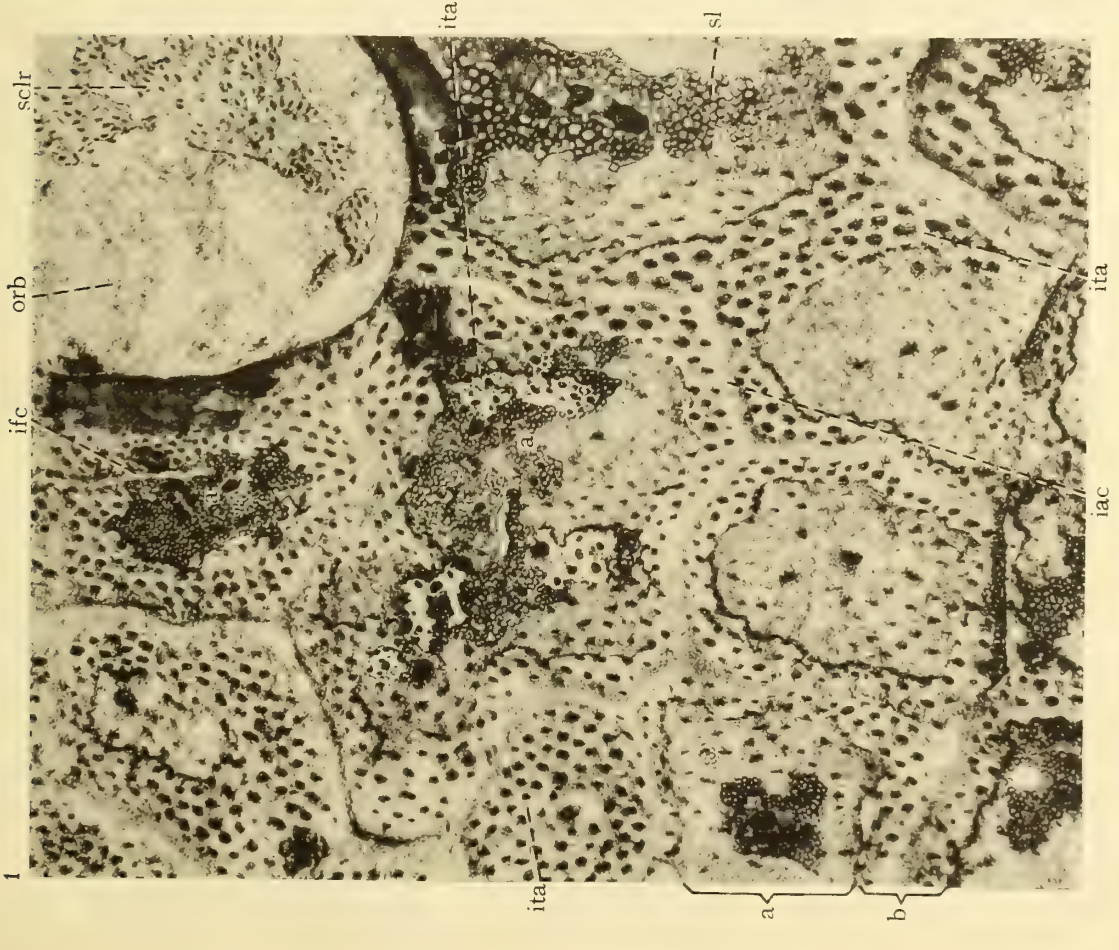

CEPHALASPIS

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PLATE 43.

Cephalaspis pagei Lankester

Fig. 1.—Almost complete specimen. The cephalic shield is represented either by parts of its dorsal exoskeleton, which is seen from the inside, or by the impression of its dorsal surface. The anterior half of the trunk is shown mainly as an impression of the lateral and ventro-lateral scales of the left side, but posteriorly the trunk is more completely preserved and shows the internal surface. Lower Old Red Sandstone: Carmylie, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.138.**—J. Powrie Coll.]. Approx. × 2 diam.

Cephalaspis powriei Lankester, var. *brevicornis* nov.

Fig. 2.—Specimen doubtfully referred to this variety, showing the dorsal exoskeleton of the cephalic shield and squamation of trunk, ventral (internal) view. (See also Pl. 30, fig. 4.) Lower Old Red Sandstone: Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.162.**—J. Powrie Coll.]. Approx. × 1½ diam.

C, caudal fin; *cm*, sensory canal groove, probably corresponding to either pre-opercular or jugal sensory canal of fishes; *cmm*, sensory canal groove, probably corresponding to middle head-line of pit-organs of fishes; cmm_1, sensory canal groove, probably corresponding to either posterior head-line of pit-organs or supra-temporal cross-commissure of fishes; D_2, dorsal fin; *dls*, dorso-lateral scales; *dsf*, dorsal electric field; *d.sp*, dorsal spine (mainly in impression); *ifc*, infra-orbital sensory canal groove; ifc_1, anterior division of infra-orbital sensory canal groove, which probably represents supra-orbital sensory canal of fishes; *lc*, groove representing cephalic division of main lateral line of fishes; *ls*, lateral scales; *lsf*, lateral electric field; *mc*, mucous canals; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *Pec*, pectoral fin; *pd*, pineal depression; pin_2, pineal opening in pineal plate; *Ppl*, pineal plate; *ps*, pectoral sinus; *vhp*, squamation of fin-membrane supported by ventral axis of caudal fin; *vrs*, ventro-lateral scales.

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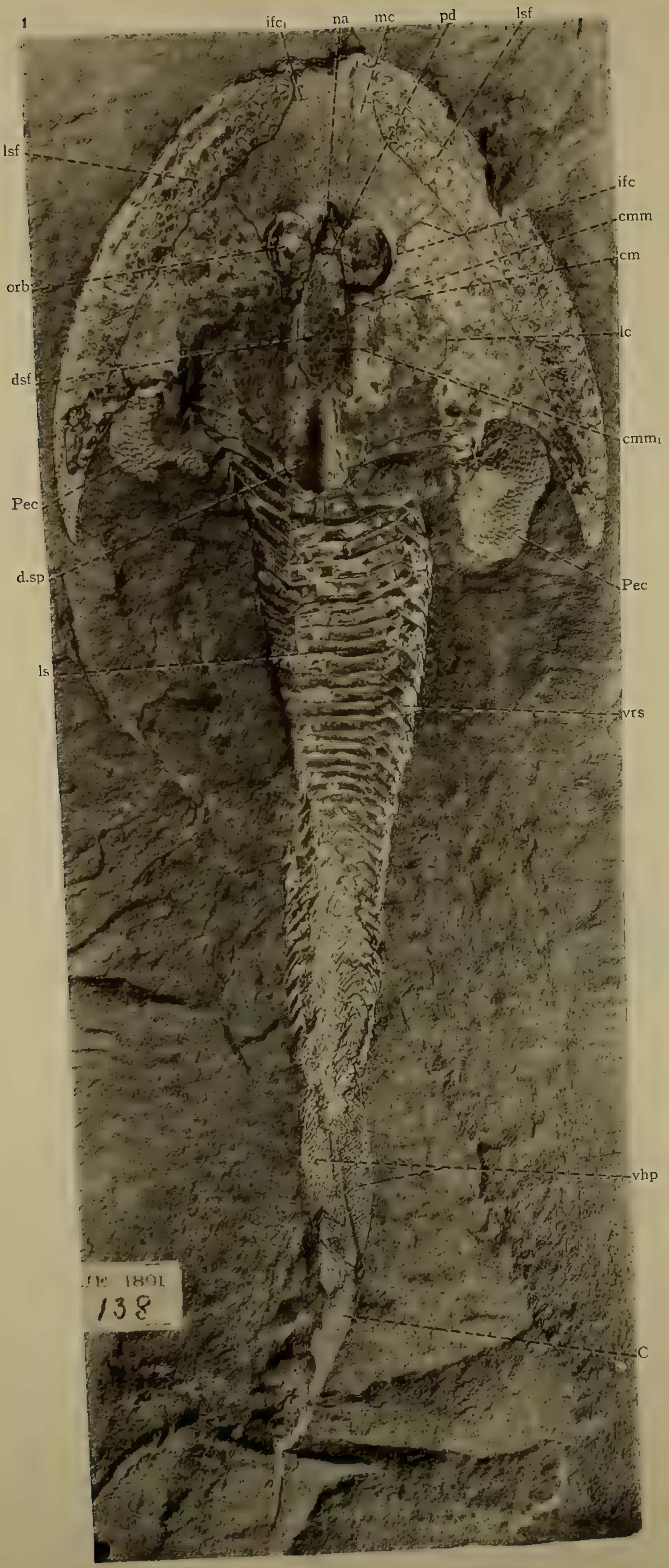

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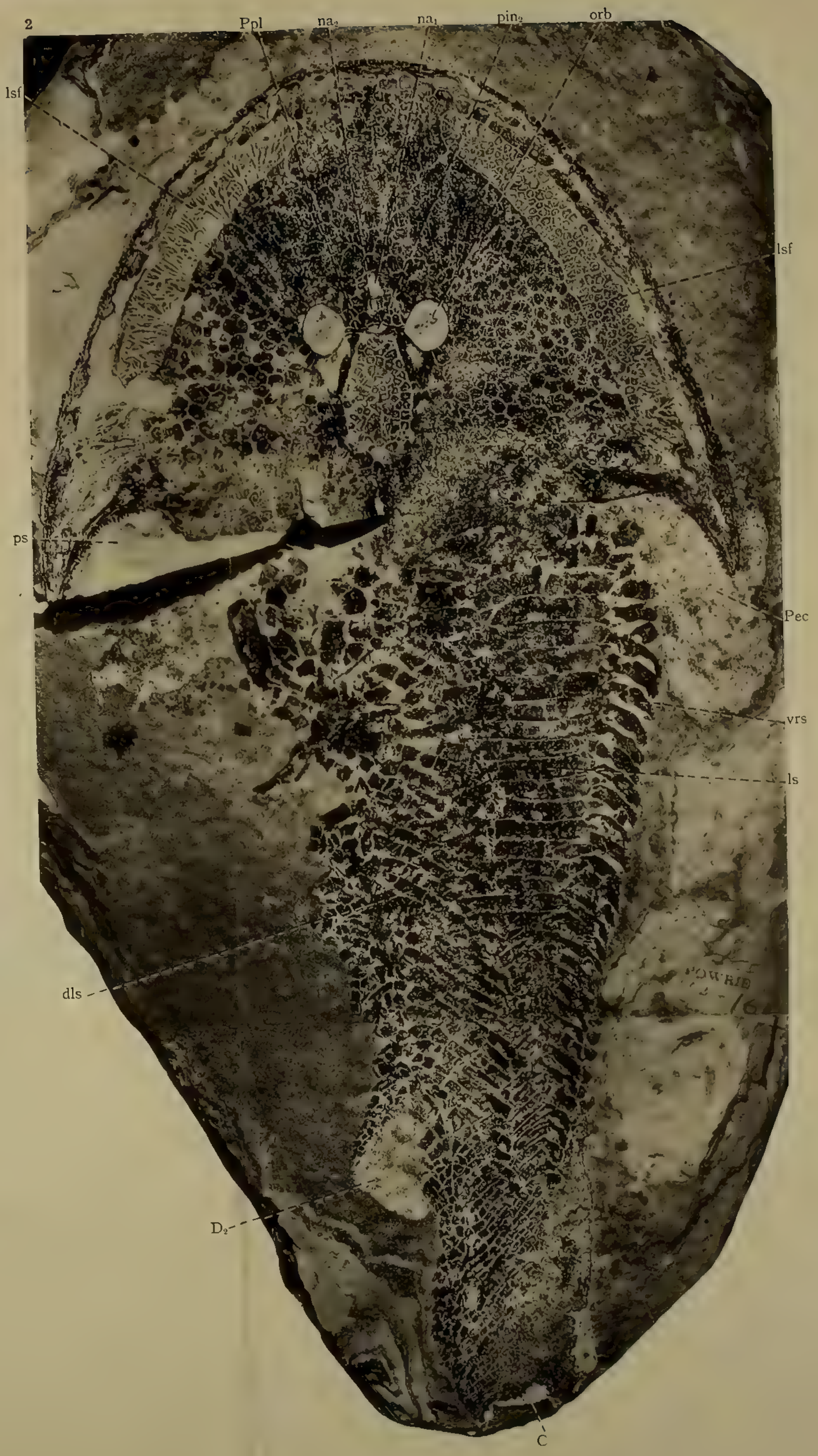

CEPHALASPIS

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PLATE 44.

Cephalaspis pagei Lankester.

Fig. 1.—Transverse section through dorsal exoskeleton of cephalic shield of specimen in which the superficial layer forms a continuous covering of middle layer. Lower Old Red Sandstone: Tealing, Forfarshire. British Museum [no. **P. 6951***a*.—Hugh Mitchell Coll., 1893]. Approx. × 50 diam.

Cephalaspis powriei Lankester, forma typica.

Fig. 2.—Part of dorsal exoskeleton of cephalic shield close to antero-lateral border of orbital opening, dorsal view. The superficial layer and most of the middle layer, except certain parts with fragments of the radiating canals, are wanting. The specimen has been made transparent by means of xylol. (Same specimen, the Lectotype, as in Pl. 27, fig. 1.) Approx. × 15 diam.

Fig. 3.—Part of dorsal exoskeleton from posterior end of same specimen, dorsal view. The middle layer is largely, and the superficial layer entirely, lacking (of the middle layer only the basal parts with a few radiating canals are to be seen here and there). Made transparent by means of xylol. Approx. × 15 diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals; *ebc*, external branches of radiating canals; *mc*, mucous canals; *ml*, middle layer of exoskeleton; *orb*, orbital opening; *p*, pores of mucous canals ascending through superficial layer; *rad.c*, radiating vascular canals; *r.sin*, venous ring-sinuses in basal layer of exoskeleton; *sl*, superficial layer of exoskeleton.

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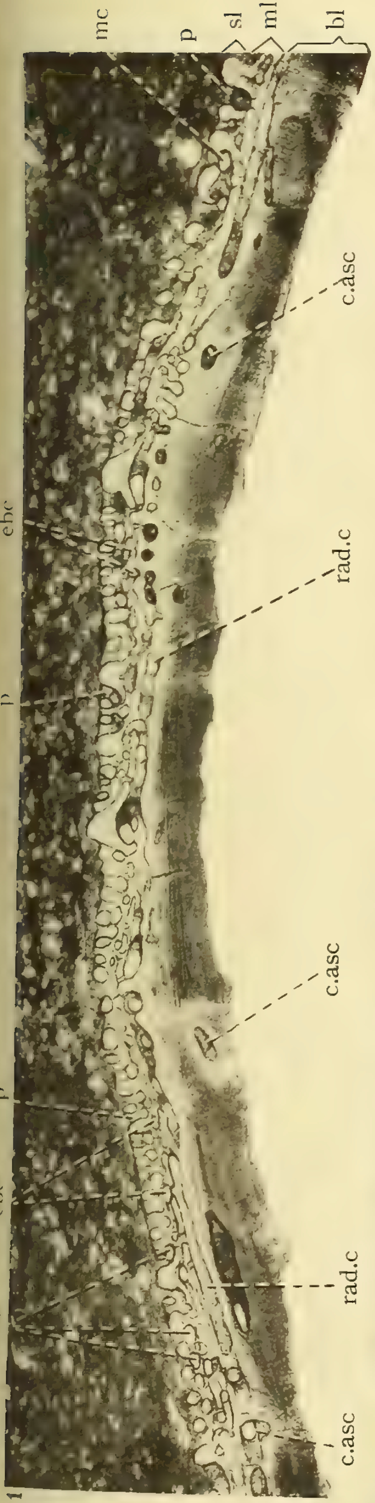

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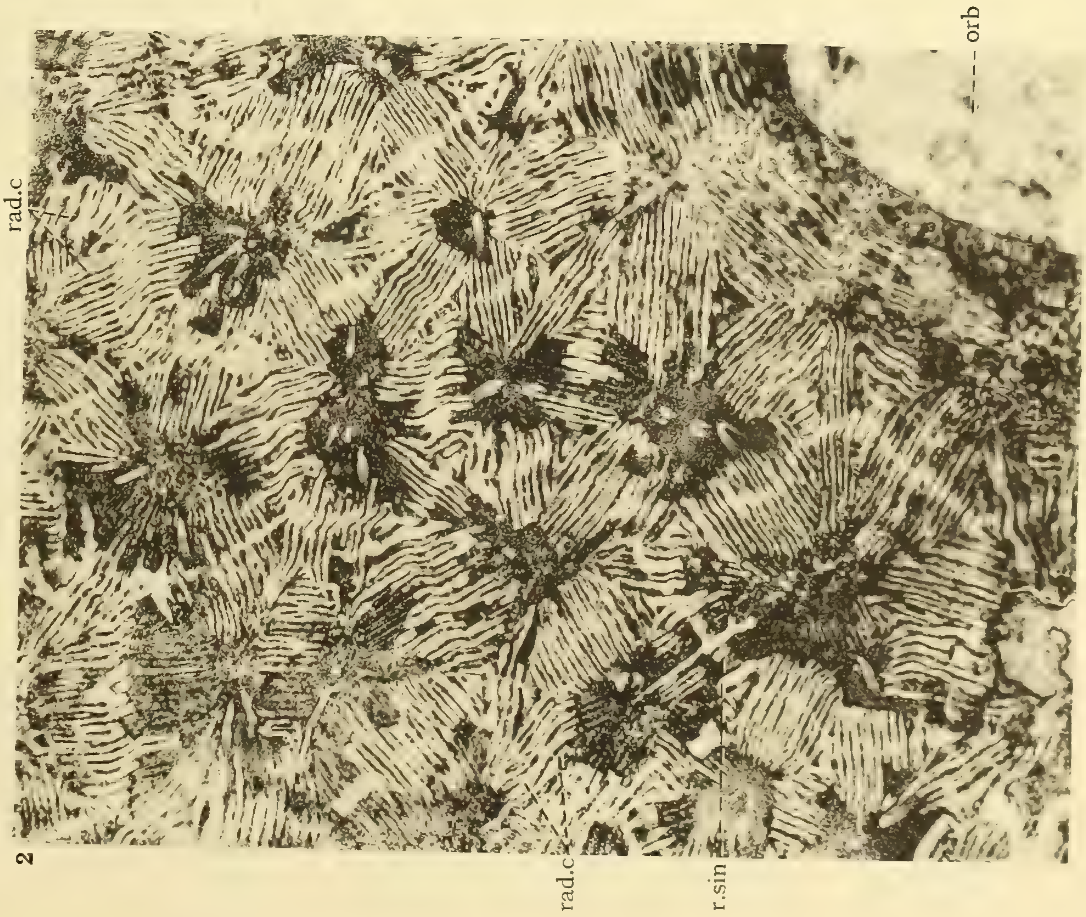

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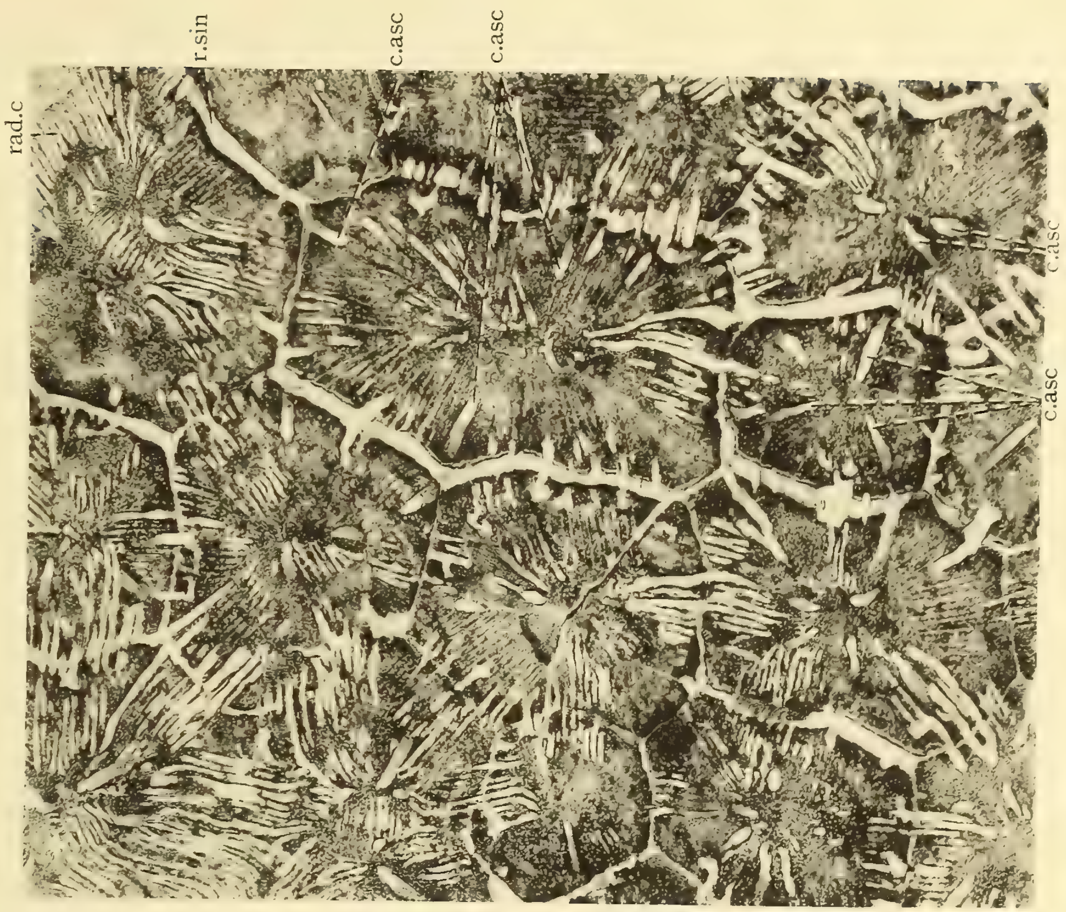

CEPHALASPIS

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PLATE 45.

Didymaspis grindrodi Lankester.

FIG. 1.—Transverse section through ventral exoskeleton of cephalic shield, in posterior half of interzonal part; external surface upwards. (See also Pl. 54, fig. 4.) Downtonian: Man Brook, Trimpley, Worcestershire. Naturhistoriska Riksmuseum, Stockholm [no. **P. 10.**—W. W. King Coll.]. × 55 diam.

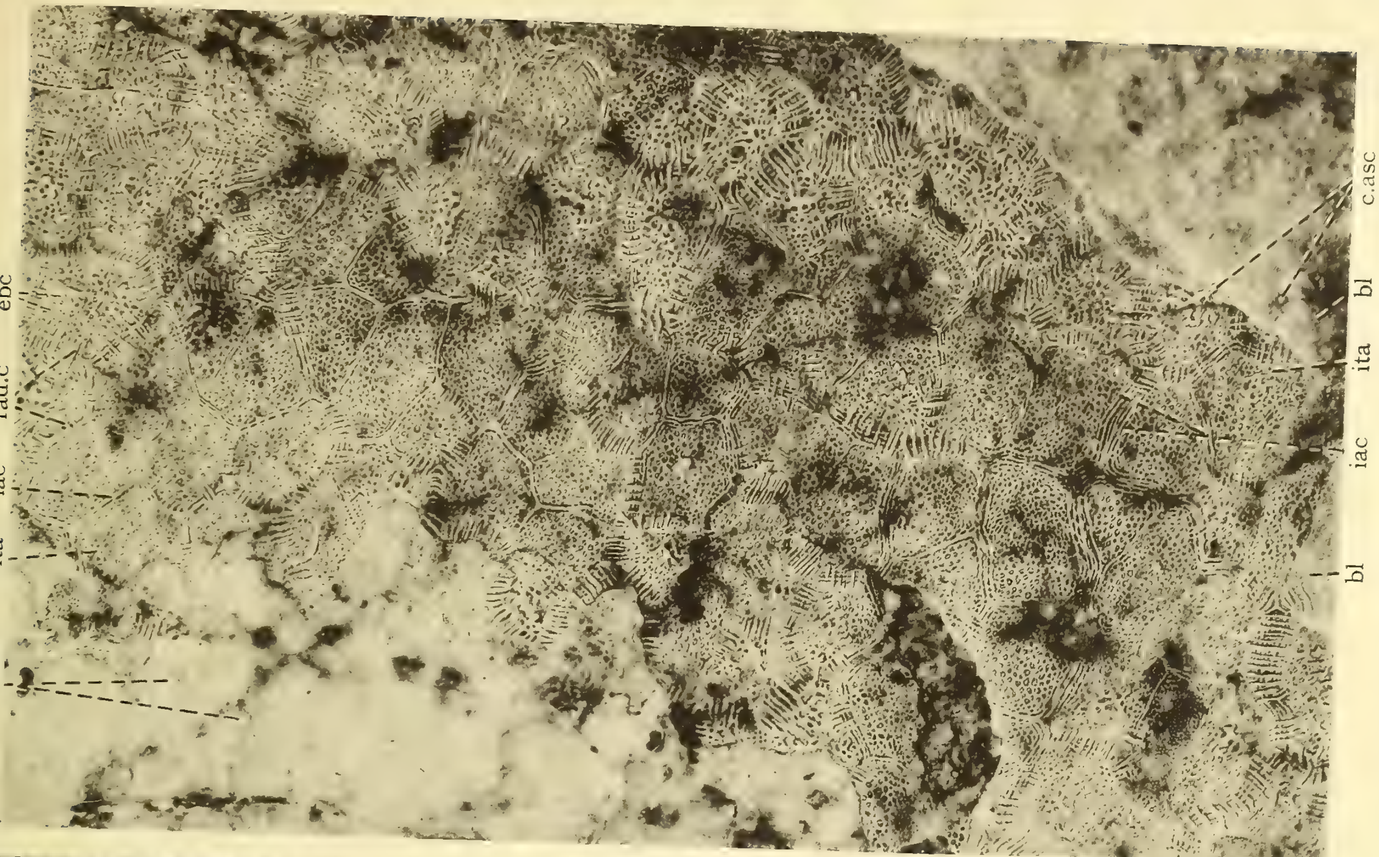
Cephalaspis campbelltonensis Whiteaves.

FIG. 2.—Mucous canal system in dorsal exoskeleton of cephalic shield, ventral view. Lower Devonian: Canada. Royal Scottish Museum, Edinburgh [no. **1887.20.49.**]. Approx. × 12 diam.

Cephalaspis sp.

FIG. 3.—Mucous canal system in dorsal exoskeleton of cephalic shield, ventral view. The basal layer has been removed where the mucous canal system is exposed, but the middle layer is present here and there, where its canals may be observed. (See also Pl. 59, fig. 3; Pl. 64, figs. 2, 3.) Lower Old Red Sandstone: Oakley Park, near Ludlow, Shropshire. British Museum [no. **35997.**—Purchased, 1861]. Approx. × 18 diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals; *ebc*, external branches of radiating canals, here passing into dentine canals; *iac*, inter-areal mucous canals; *ita*, intra-areal mucous canals; *rad.c*, radiating canals.



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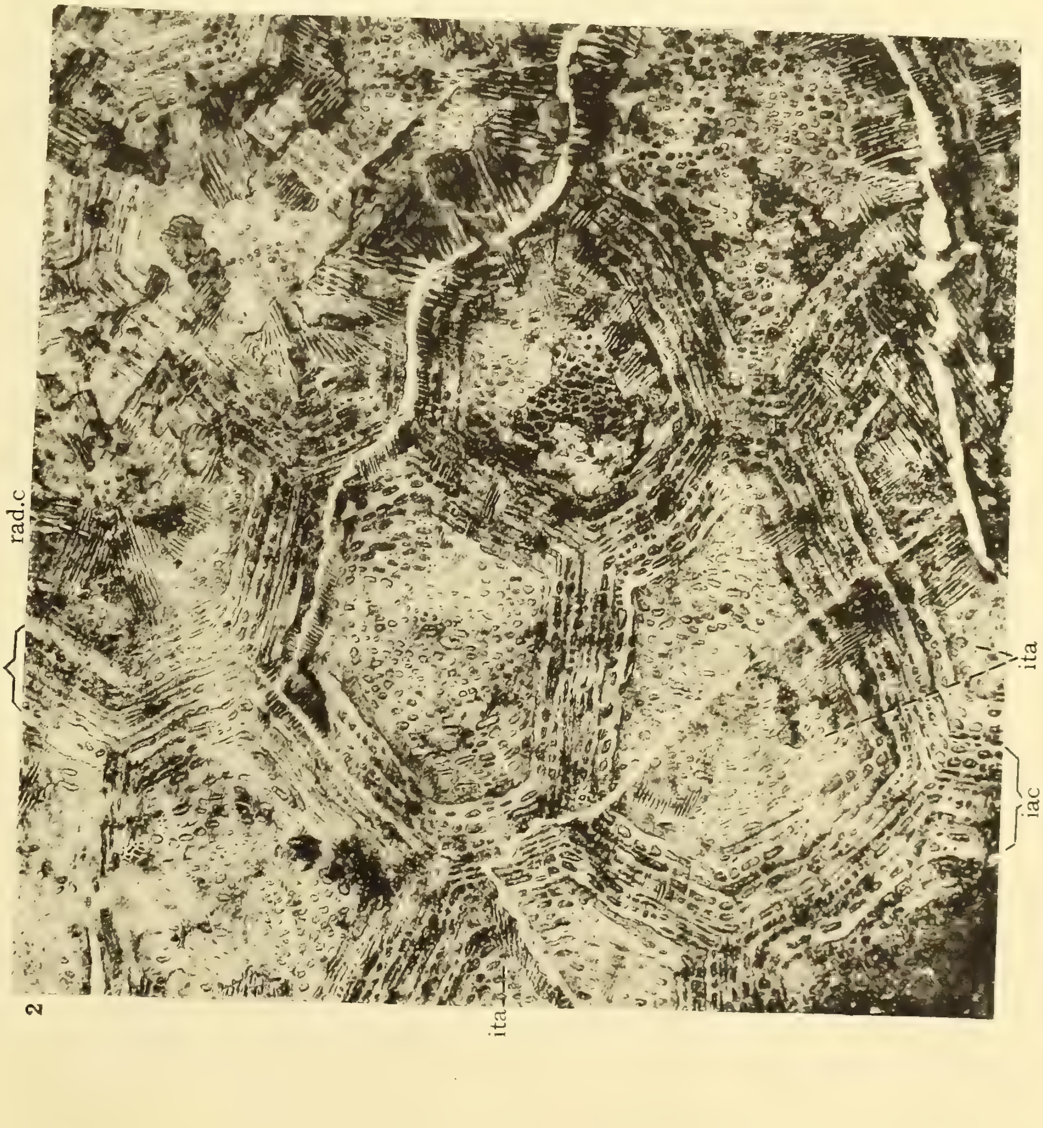

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DIDYMASPIS and CEPHALASPIS

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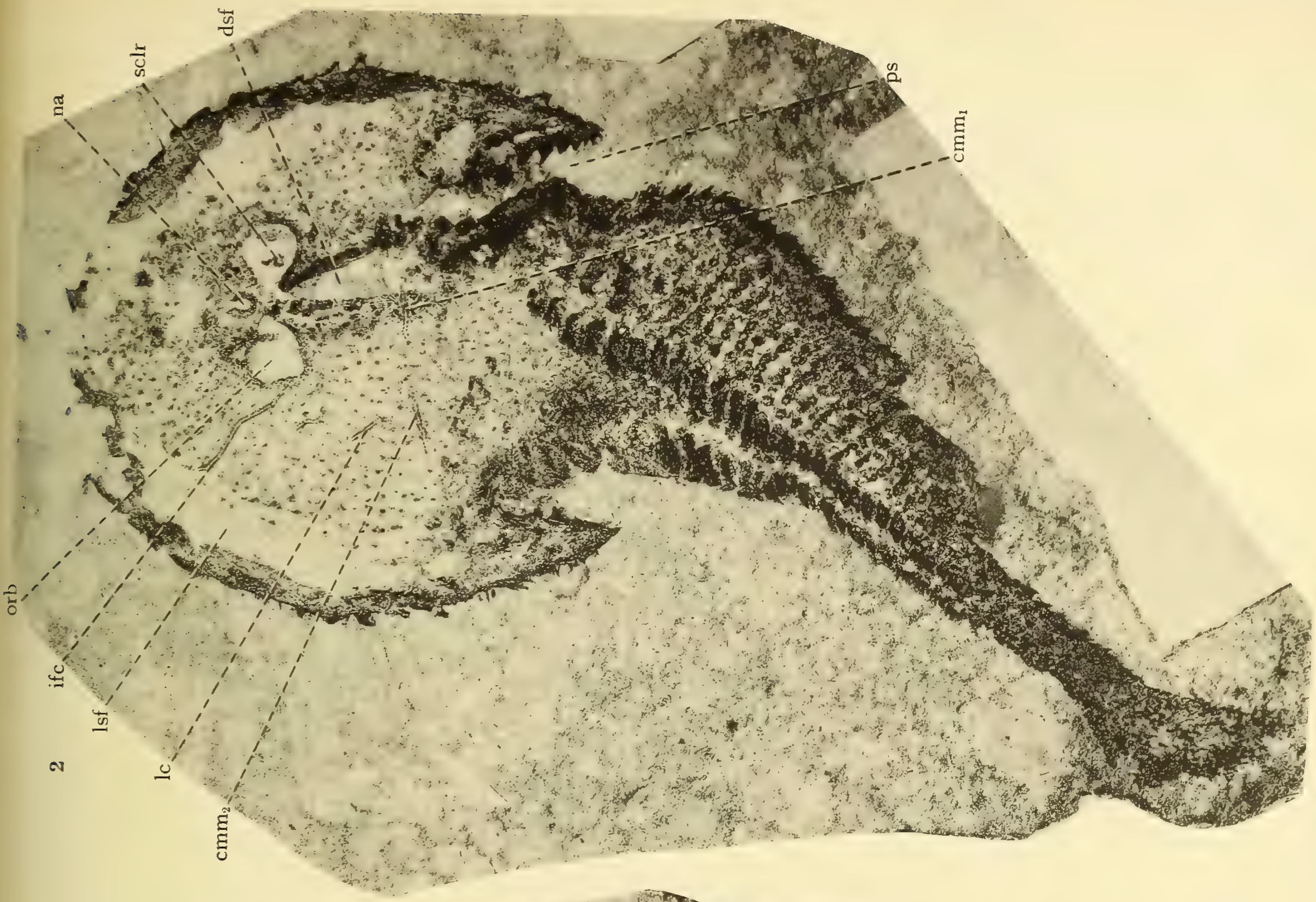
PLATE 46.

Cephalaspis spinifer, sp. nov.

FIGS. 1, 2.—Fairly complete but much-crushed and distorted specimen in counterpart. Lower Old Red Sandstone: Turin Hill, Forfarshire. HOLOTYPE. (Fig. 1) Royal Scottish Museum, Edinburgh [no. **1891.92.149.**—J. Powrie Coll.]. (Fig. 2) British Museum [no. **P. 16146.**—Kinnaird Coll., *ex* Coll. Dundee Museum, 1932]. × 4 diam.

cmm_1, cmm_2, sensory canal groove corresponding either to posterior head-line of pit-organs or to supratemporal cross-commissure of fishes; *dsf,* dorsal electric field; *ifc,* infra-orbital sensory canal groove; *lc,* sensory canal grooves corresponding to cephalic division of main lateral line of fishes; *ls,* lateral scales; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; *orb,* orbital opening; *ps,* pectoral sinus; *sclr,* sclerotic ring (dorsal part).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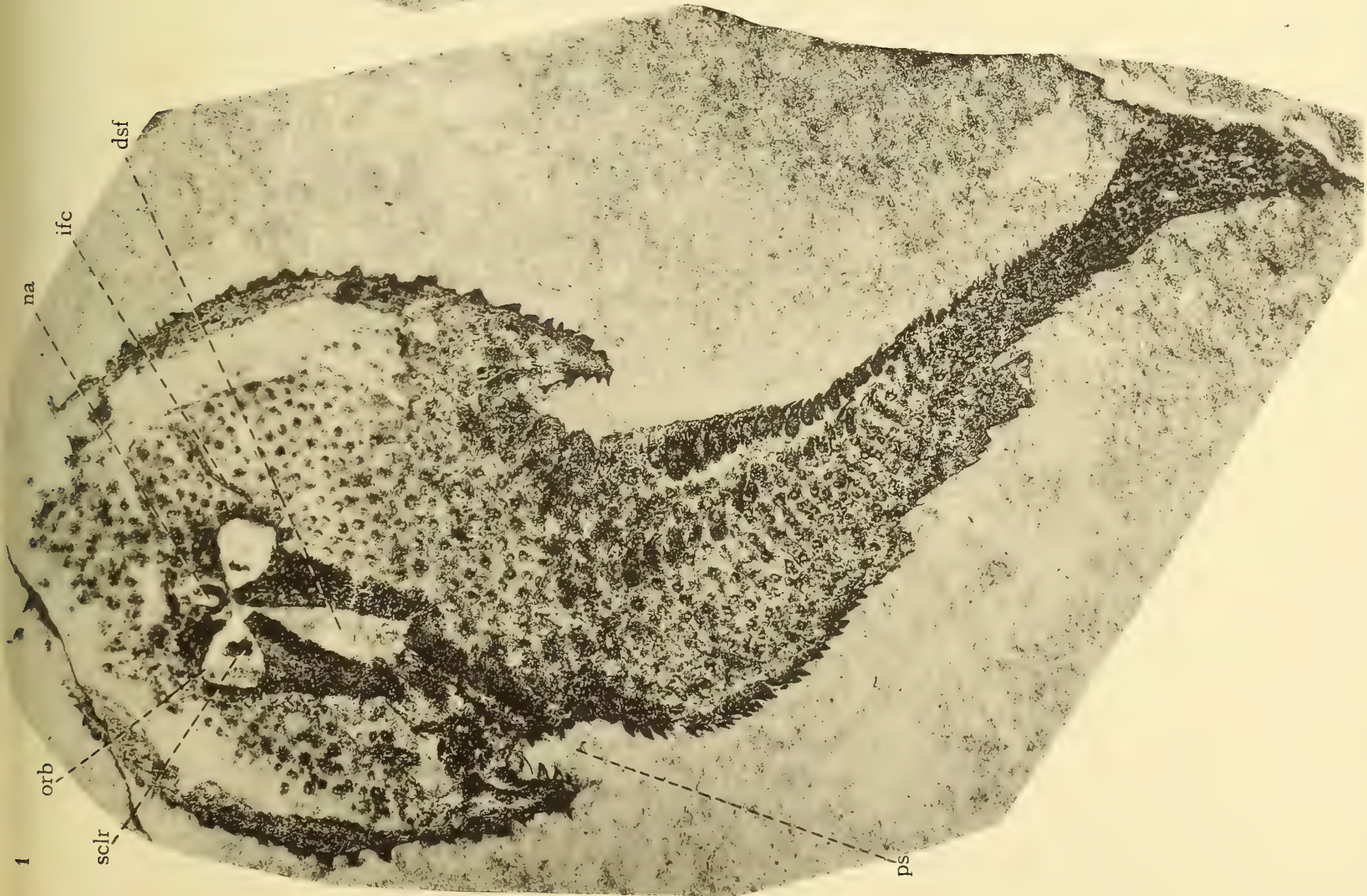
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CEPHALASPIS

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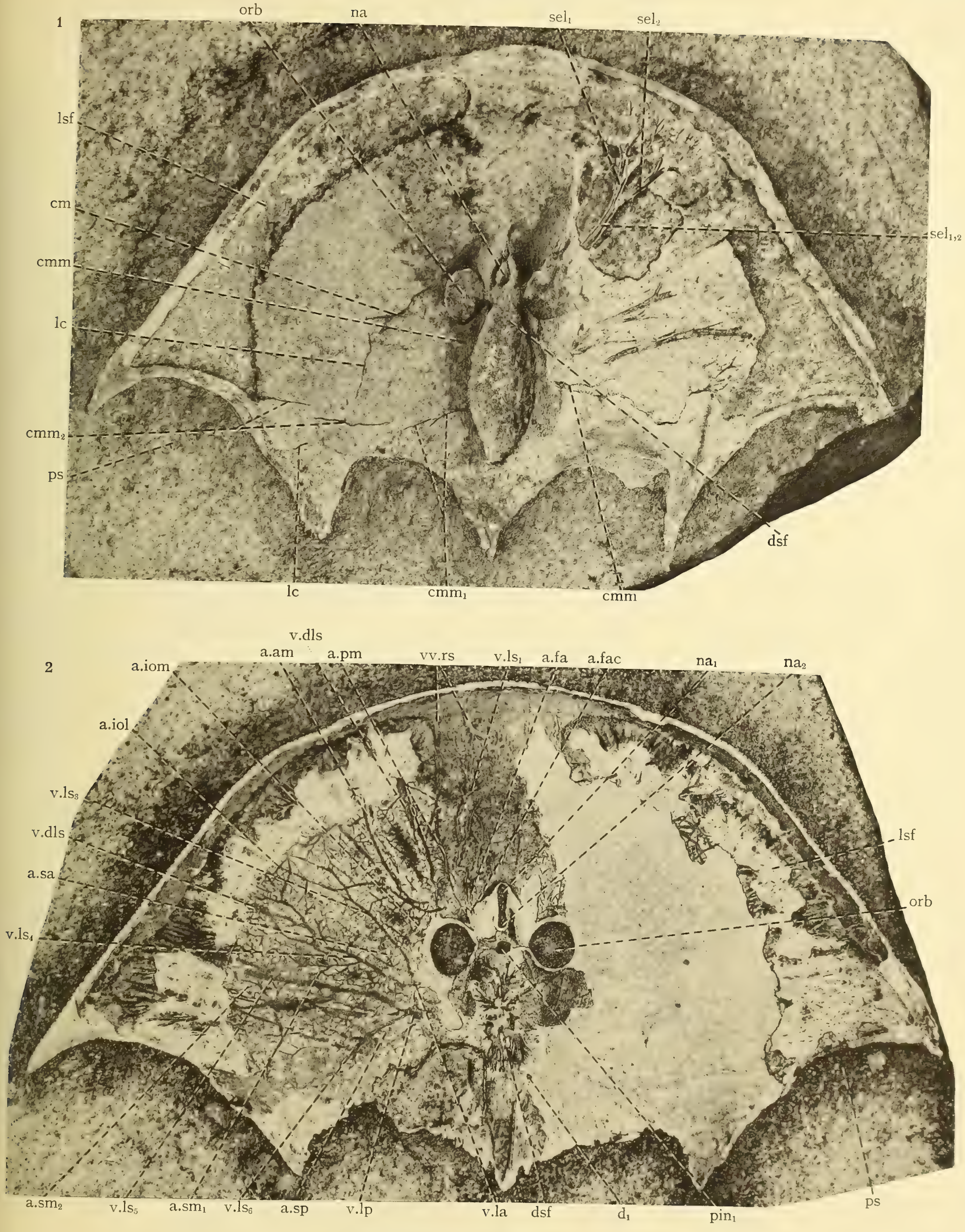
PLATE 47.

Benneviaspis lankesteri, sp. nov.

Fig. 1.—Dorsal exoskeleton of cephalic shield, ventral view. On the left side of the figure certain superficial parts only are present. Lower Old Red Sandstone: Cradley, Herefordshire. Geol.-Pal. Museum, of the University of Berlin [not numbered]. × 3 diam.

Fig. 2.—Cephalic shield, dorsal view. On the right side the exoskeleton has to a great extent been removed in order to show the main canals of the sub-aponeurotic (sub-cutaneous) vascular plexus. (See also text-fig. 11.) Lower Old Red Sandstone: Cradley, Herefordshire. Holotype. British Museum [no. **46877.**—Purchased, 1875]. × 3 diam.

a.am, mandibular branch of canal of a. facialis; *a.fa*, anterior branch of canal of a. facialis; *a.fac*, canal of a. facialis; *a.iol*, lateral infra-orbital branch of canal of a. facialis; *a.iom*, medial infra-orbital branch of canal of a. facialis; *a.pm*, pre-mandibular branch of canal of a. facialis; *a.sa*, *a.sm*$_1$, *a.sm*$_2$, *a.sp*, canals of dorso-lateral superficial arteries 1–4; *cm*, sensory canal groove probably representing either pre-opercular or jugal sensory canal of fishes; *cmm*, sensory canal groove representing middle head-line of pit-organs of fishes; *cmm*$_1$, *cmm*$_2$, sensory canal groove representing either posterior head-line of pit-organs or supra-temporal cross-commissure of fishes; *d*$_1$, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *dsf*, dorsal electric field; *lc*, sensory canal grooves corresponding to cephalic division of main lateral line of fishes; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *na*$_1$, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); *na*$_2$, posterior division of naso-hypophysial aperture (nasal opening proper); *orb*, orbital opening; *pin*$_1$, pineal opening on dorsal surface of endoskeleton of cephalic shield; *ps*, pectoral sinus; *sel*$_1$, *sel*$_2$, canals of nerves 1 and 2 of lateral electric field; *sel*$_{1,2}$, common canal of two most anterior nerves of lateral electric field; *v.dls*, canals of veins which carried blood down to lateral electric field; *v.la*, canal of common trunk of dorso-lateral superficial veins 3 and 4; *v.lp*, canal of common trunk of dorso-lateral superficial veins 5 and 6; *v.ls*$_1$, *v.ls*$_3$–*v.ls*$_6$, canals of dorso-lateral superficial veins 1 and 3–6; *vv.rs*, canals of rostral veins.



BENNEVIASPIS

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PLATE 48.

Benneviaspis sp.

FIG. 1.—Imperfect cephalic shield, dorsal view. The exoskeleton has been removed to show the canals of the sub-aponeurotic (sub-cutaneous) vascular plexus and some of the nerve-canals. (See also text-fig. 12.) Lower Old Red Sandstone: Cradley, Herefordshire. Royal Scottish Museum, Edinburgh [no. **1890.6.29***a*]. × 3 diam.

Benneviaspis anglica, sp. nov.

FIG. 2.—Cephalic shield, dorsal view. The exoskeleton has been removed to a great extent to show the main vascular canals of the sub-aponeurotic (sub-cutaneous) vascular plexus and certain nerve-canals. (See also text-fig. 10.) Lower Old Sandstone: Cradley, Herefordshire. HOLOTYPE. British Museum [no. **46568.**—Purchased, 1875]. × 3 diam.

a.am, mandibular branch of canal of a. facialis; *a.fa,* anterior branch of canal of a. facialis; *a.fac,* canal of a. facialis; *a.iol,* lateral infra-orbital branch of canal of a. facialis; *a.iom,* medial infra-orbital branch of canal of a. facialis; *a.la,* canal of common trunk of dorso-lateral superficial arteries 1 and 2; *a.pm,* pre-mandibular branch of canal of a. facialis; *a.sa,* $a.sm_1$, $a.sm_2$, *a.sp,* canals of dorso-lateral superficial arteries 1–4; d_1, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *dsf,* dorsal electric field; *lsf,* lateral electric field; *na,* naso-hypophysial aperture; *orb,* orbital opening; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps,* pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field; $sel_{1,\,2}$, common canal of two most anterior nerves of lateral electric field; $v.cl_1$, pre-orbital division of canal of v. capitis lateralis; *v.dls,* canals of veins which carried blood to lateral electric field; *v.la,* canal of common trunk of dorso-lateral superficial veins 3 and 4; $v.ls_1$–$v.ls_6$, canals of dorso-lateral superficial veins 1–6; *v.lp,* canal of common trunk of dorso-lateral superficial veins 5 and 6; *vv.rs,* canals of rostral veins; V_1, canal of n. profundus; V_2, canal of n. trigeminus proper; *VII,* canal of n. facialis (from labyrinth cavity to oralo-branchial chamber).

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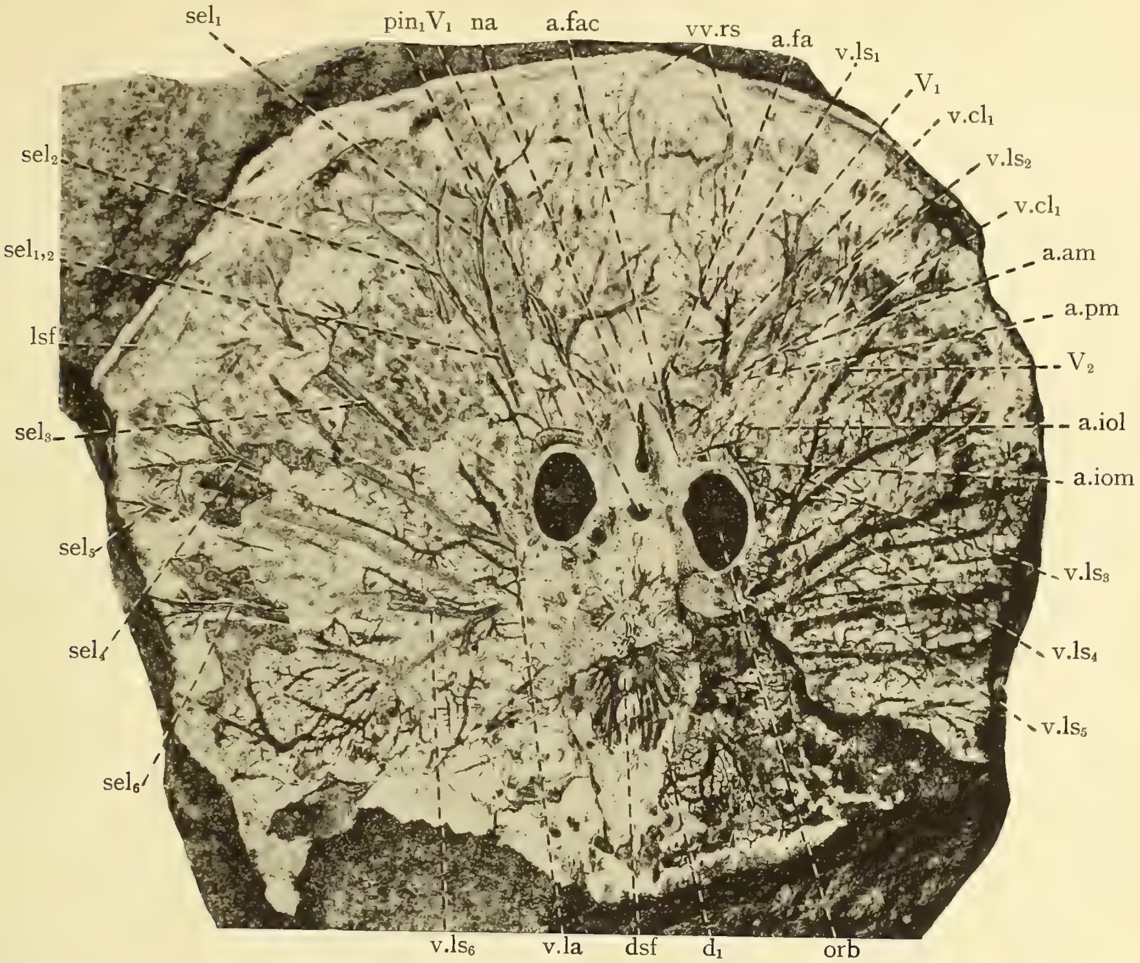

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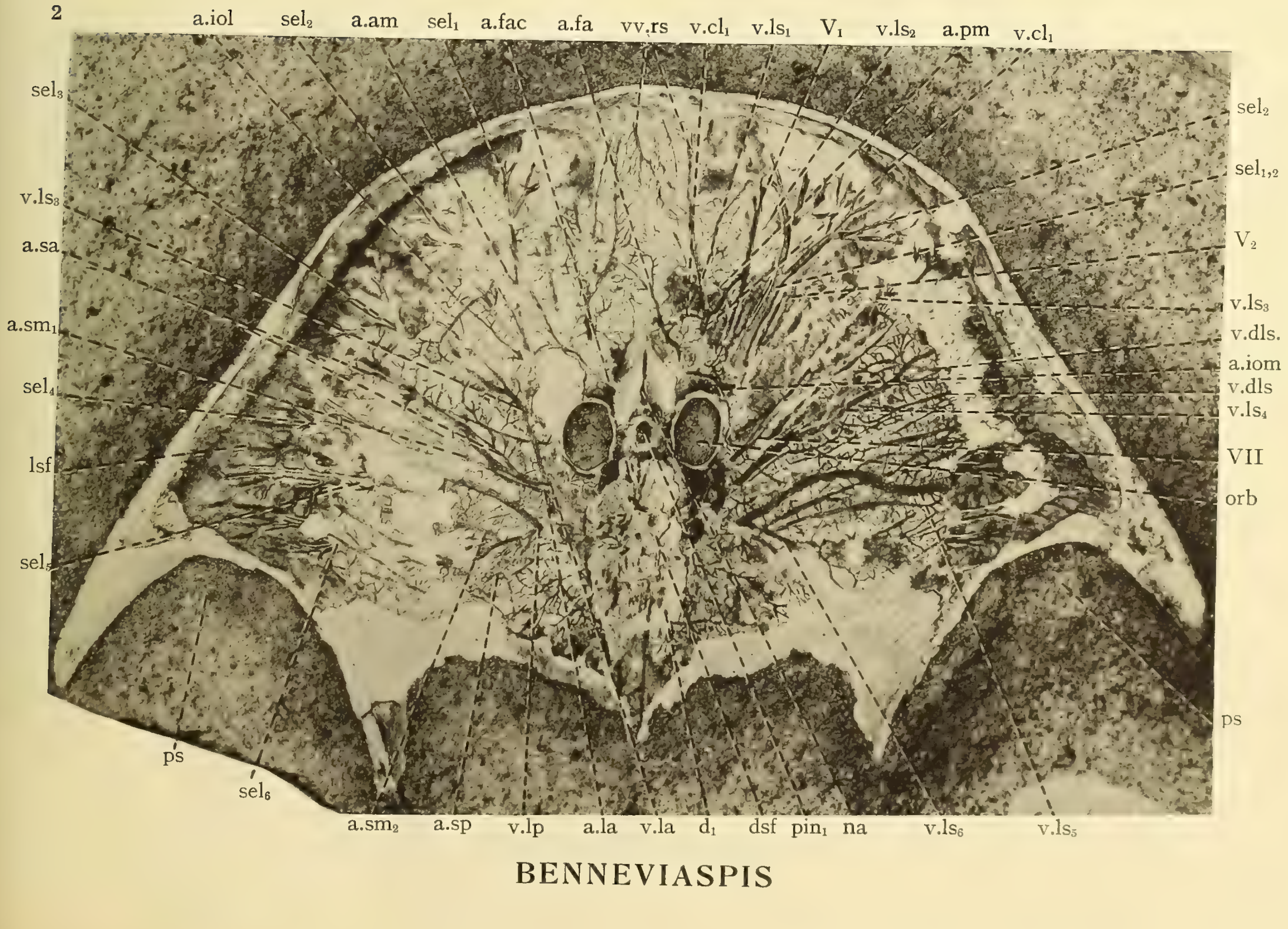

BENNEVIASPIS

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PLATE 49.

Securiaspis kitchini, gen. et sp. nov.

Fig. 1.—Cephalic shield, dorsal view. Only the most basal parts of the dorsal exoskeleton are preserved. Lower Old Red Sandstone: Skirrid Fawr, near Abergavenny, Monmouthshire. Holotype. British Museum [no. **P. 4115.**—D. M. McCullough Coll., 1883]. × 3 diam.

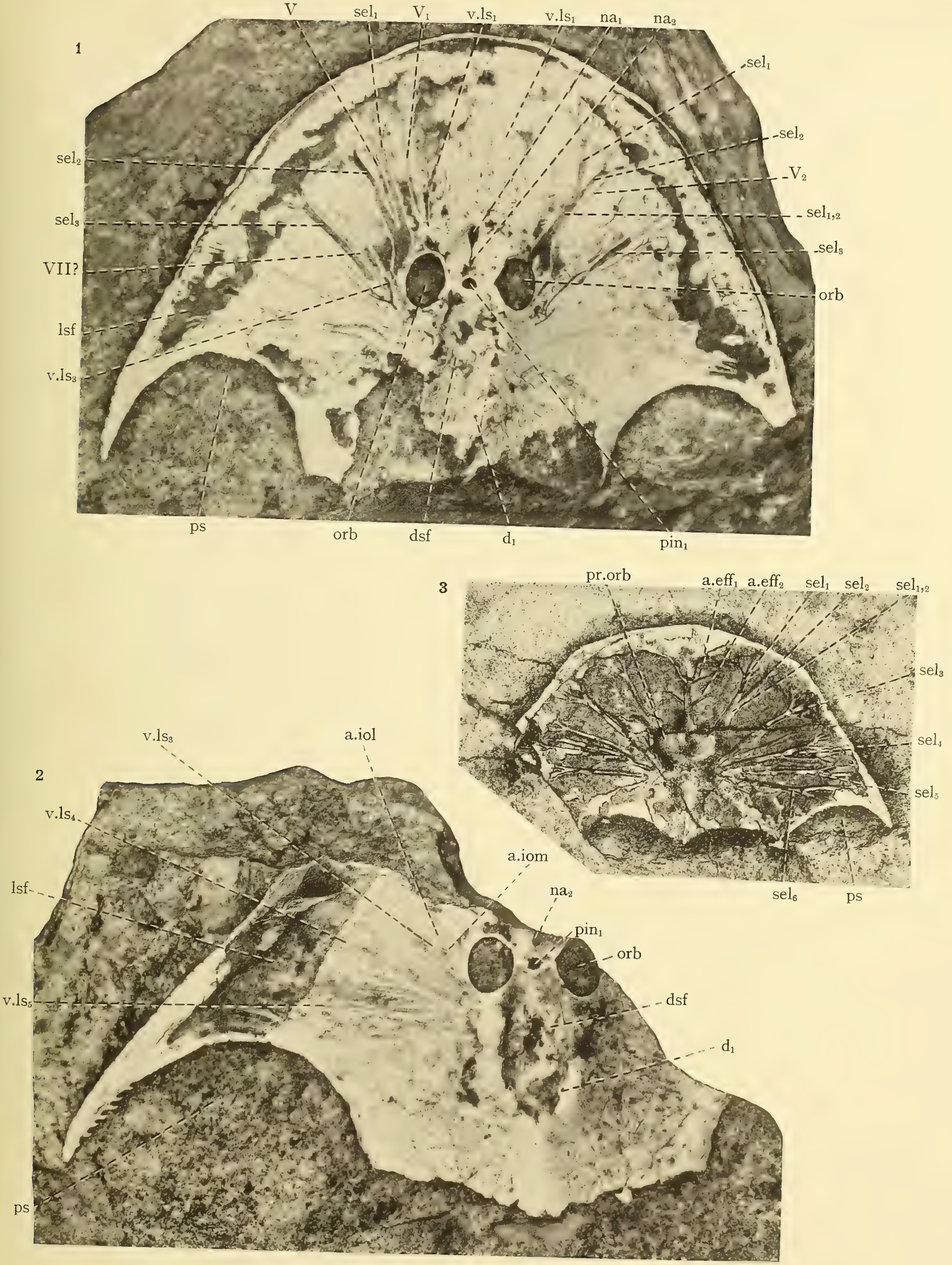
Securiaspis kingi, gen. et sp. nov.

Fig. 2.—Part of cephalic shield, dorsal view. The exoskeleton anteriorly is split off, exposing several of the vascular canals. Lower Old Red Sandstone: Leverhill, near Leominster, Herefordshire. Holotype. Museum of Practical Geology, London [no. **47792.**—J. F. Crouch Coll.]. × 3 diam.

Benneviaspis lankesteri, sp. nov.

Fig. 3.—Cephalic shield, dorsal view. The dorsal exoskeleton is almost entirely destroyed, and in the middle, parts of the endoskeleton have split off, leaving an impression of the roof of the oralo-branchial chamber. Lower Old Red Sandstone: Cradley, Herefordshire. Royal Scottish Museum, Edinburgh [no. **1890.6.29**]. Approx. × $1\frac{1}{3}$ diam.

a.iol, lateral infra-orbital branch of canal of a. facialis; *a.iom,* medial infra-orbital branch of canal of a. facialis; $a.eff_1$, $a.eff_2$, grooves of efferent branchial arteries 1 and 2; d_1, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *dsf,* dorsal electric field; *lsf,* lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *orb,* orbital opening; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *pr.orb,* impression of orbital prominence; *ps,* pectoral sinus; sel_1–sel_6, canals of nerves 1–6 of lateral electric field; $sel_{1,2}$, common canal of two most anterior nerves of lateral electric field; $v.ls_1$, $v.ls_3$–$v.ls_5$, canals of dorso-lateral superficial veins 1 and 3–5; V_1, canal of n. profundus; V_2, canal of n. trigeminus proper; *VII?*, probable canal of n. facialis (from labyrinth cavity to oralo-branchial chamber).



SECURIASPIS and BENNEVIASPIS

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PLATE 50.

Securiaspis kitchini, gen. et sp. nov.

FIG. 1.—Cephalic shield, dorsal view. The whole of the dorsal exoskeleton of the shield is lacking. Lower Old Red Sandstone (Middle Cornstones): Kentchurch Hill, Herefordshire. Sedgwick Museum, Cambridge [no. **A. 3312.**—W. Symonds Coll.]. × 2 diam.

Thyestes egertoni (Lankester).

FIG. 2.—Distorted cephalic shield, dorsal view. The dorsal exoskeleton of the shield has been largely removed. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 3237***b*.—Enniskillen Coll., 1882]. × 4 diam.

Thyestes salteri (Egerton).

FIG. 3.—Distorted cephalic shield, dorsal view. The dorsal exoskeleton of the shield is either altogether wanting or represented by an impression of the under-surface only. Downtonian (Temeside Shales): Ludlow Station, Shropshire. Ludlow Museum [no. **D/i/30.**—R. Lightbody Coll.]. × 3½ diam.

FIG. 4.—Somewhat distorted cephalic shield, dorsal view. The dorsal exoskeleton of the shield is either altogether wanting or represented by an impression of the under-surface only. Downtonian: Railway at Ludlow, Shropshire. British Museum [no. **P. 674.**—P. M. G. Egerton Coll., 1882]. × 3½ diam.

c.sem.ant, division of labyrinth cavity for canalis semicircularis anterior; *c.sem.post*, division of labyrinth cavity for canalis semicircularis posterior; d_1, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *des*, canal of nerve of dorsal electric field; *dic*, division of cavum cerebrale cranii for diencephalon; *dsf*, dorsal electric field; *k*, branchial fossae (ventral parts preserved as casts); *lsf*, lateral electric field; *mec*, division of cavum cerebrale cranii for mesencephalon; *met*, division of cavum cerebrale cranii for metencephalon; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *olm*, lateral border of occipital region of endoskeleton; *orb*, orbital opening or orbital cavity; *otl*, posterior margin of endoskeleton of otic region passing laterally into medial margin of endoskeletal shoulder-girdle, medially into lateral margin of endoskeleton of occipital region; *pin*, pineal canal; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; $sel_{1,2}$, common canal of two most anterior nerves of lateral electric field; sel_3–sel_6, canals of nerves 3–6 of lateral electric field; *tel*, division of cavum cerebrale cranii for telencephalon; *v.cl*, canal of post-orbital division of v. capitis lateralis; $v.cl_1$, canal of pre-orbital division of v. capitis lateralis; *vest*, vestibular division of labyrinth cavity; $v.ls_1$–$v.ls_3$?, supposed canals of dorso-lateral superficial veins 1–3; $v.ls_4? + v.ls_5?$, canal either for dorso-lateral superficial vein 4 or for dorso-lateral superficial veins 4 and 5; $v.ls_6$?, canal probably for dorso-lateral superficial vein 6; *v.marg*, canal of marginal vein; V_1, canal of n. profundus; V_2, canal of n. trigeminus proper.

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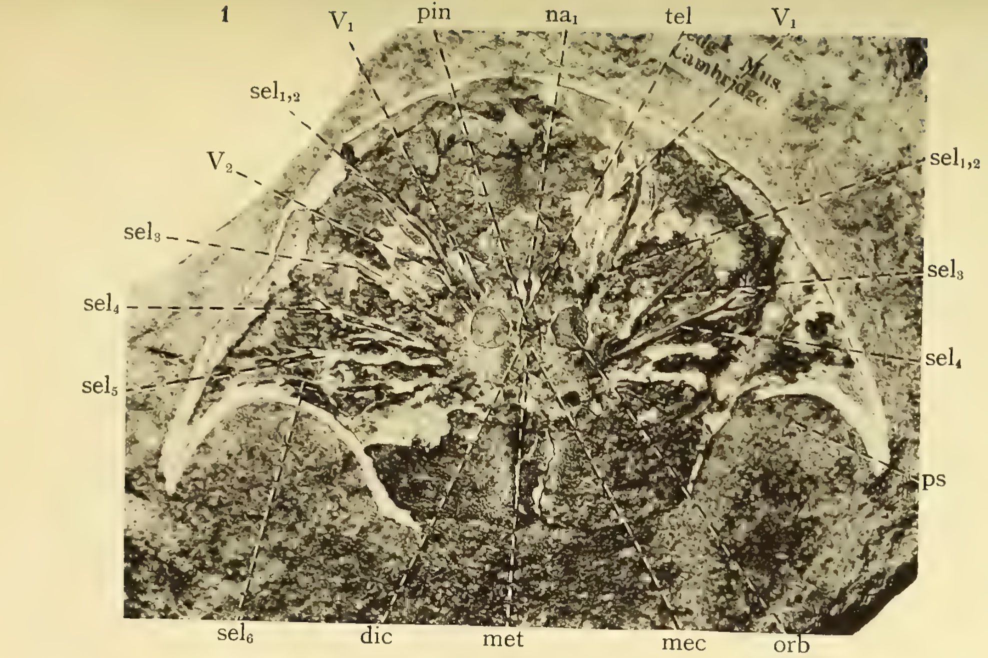

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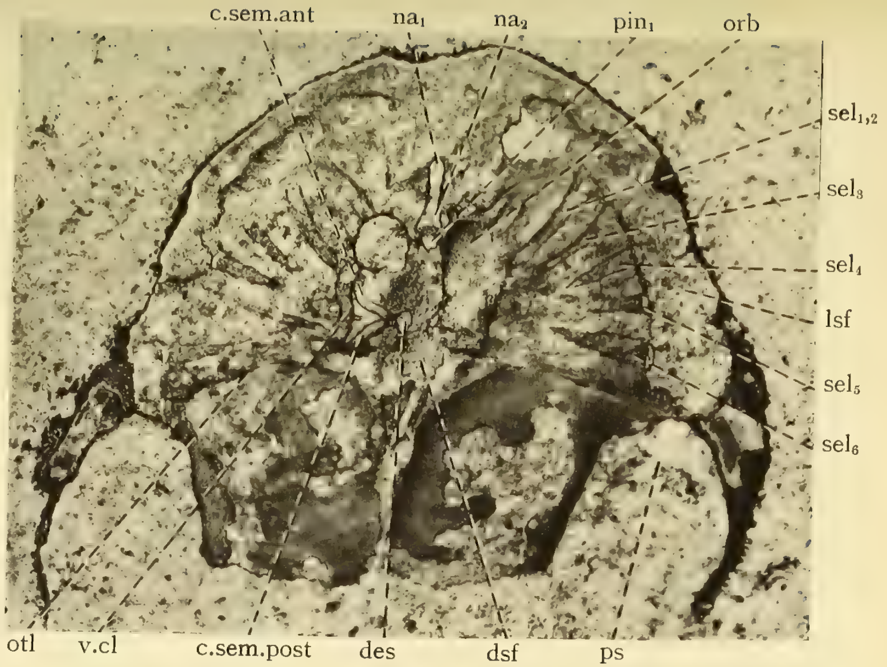

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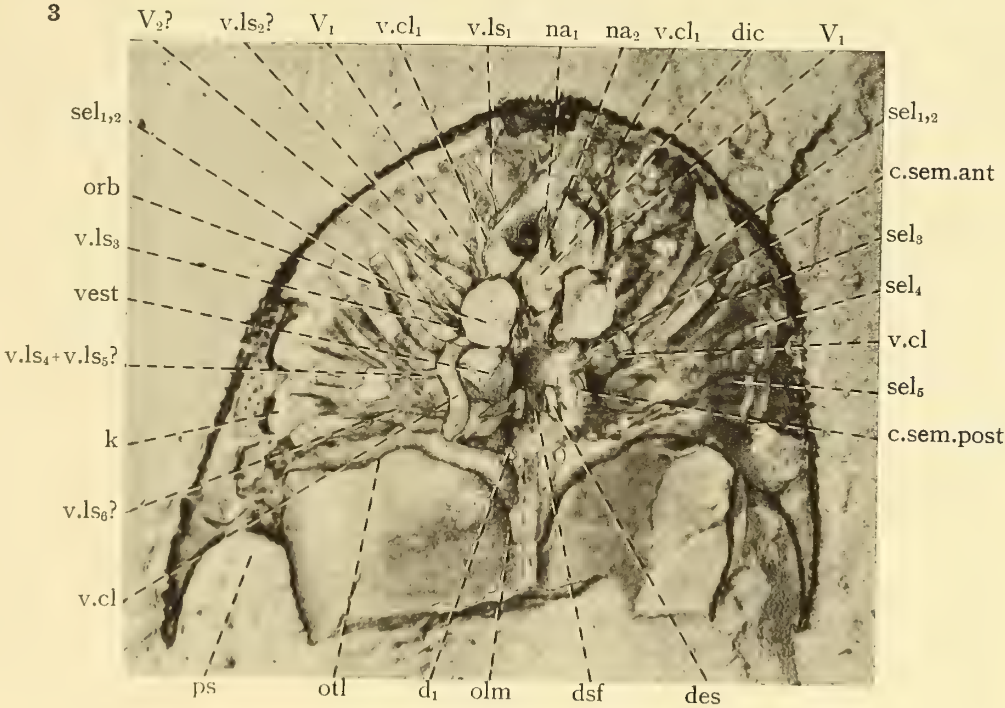

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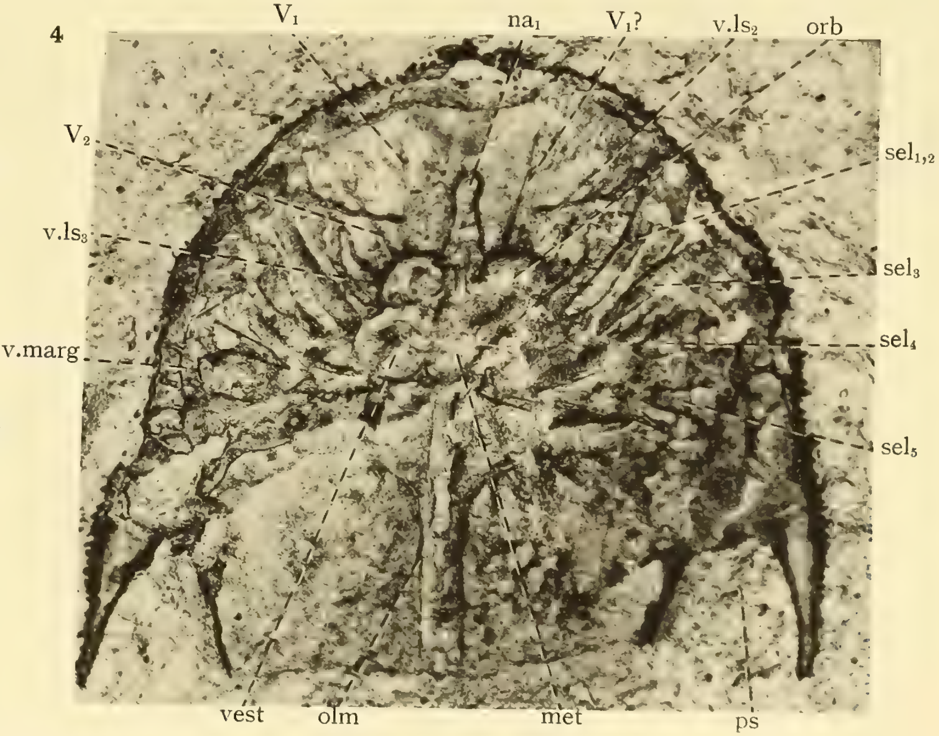

SECURIASPIS and THYESTES

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PLATE 51.

Thyestes egertoni (Lankester).

FIG. 1.—Cephalic shield, dorsal view. The dorsal exoskeleton has to a great extent been removed. Downtonian: Ledbury, Herefordshire. British Museum [no. **P. 6113***a*.—G. H. Piper Coll., 1889]. × 4 diam.

FIG. 2.—Cephalic shield, dorsal view. The dorsal exoskeleton has to a great extent been removed. (See also text-fig. 13). Downtonian (Grey Grits): Ledbury Station, Herefordshire. British Museum [no. **P. 8831***a*.—G. H. Piper Coll., 1898]. × < 7 diam.

FIG. 3.—Posterior part of cephalic shield with large part of trunk, dorsal view. The posterior margin of the inter-zonal part and its relations to the scales are well displayed. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 5316.**—G. H. Piper Coll., 1887]. × > 3 diam.

FIG. 4.—Posterior part of cephalic shield of same specimen, ventral view. × 3 diam.

FIG. 5.—Cephalic shield, dorsal view. The dorsal exoskeleton of the shield has to a great extent been removed. Downtonian: Ledbury, Herefordshire. British Museum [no. **46954.**—Purchased, 1876]. × 2 diam.

a.dsm?, canal probably of post-orbital superficial artery; *com*, commissural division of labyrinth cavity; *c.sem.ant*, division of labyrinth cavity for canalis semicircularis anterior; *c.sem.post*, division of labyrinth cavity for canalis semicircularis posterior; *d*$_2$, canal probably for vein from dorsal electric field and perhaps also for ductus endolymphaticus; *des*, canal of nerve of dorsal electric field; *dsf*, dorsal electric field; *f.cn*, fossa circum-nasalis; *ls*, lateral scales; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; *olm*, lateral border of occipital region of endoskeleton; *orb*, orbital opening; *otl*, posterior margin of endoskeleton of otic region, passing laterally into medial margin of endoskeletal shoulder-girdle, and medially into lateral margin of endoskeleton of occipital region; *pin*$_1$, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; *rs*, dorsal ridge-scales; *sel*$_{1,\,2}$, common canal of two most anterior nerves of lateral electric field; *sel*$_3$–*sel*$_5$, canals of nerves 3–5 of lateral electric field; *v.cl*, post-orbital division of canal of v. capitis lateralis; *v.cl*$_1$, pre-orbital division of v. capitis lateralis; *v.ls*$_1$–*v.ls*$_6$, canals of dorso-lateral superficial veins 1–6; *vv.es*, plates of ventral visceral exoskeleton; V_1, canal of n. profundus; V_2?, canal probably of n. trigeminus proper; *VII*, canal probably of n. facialis (from labyrinth cavity to oralo-branchial chamber).

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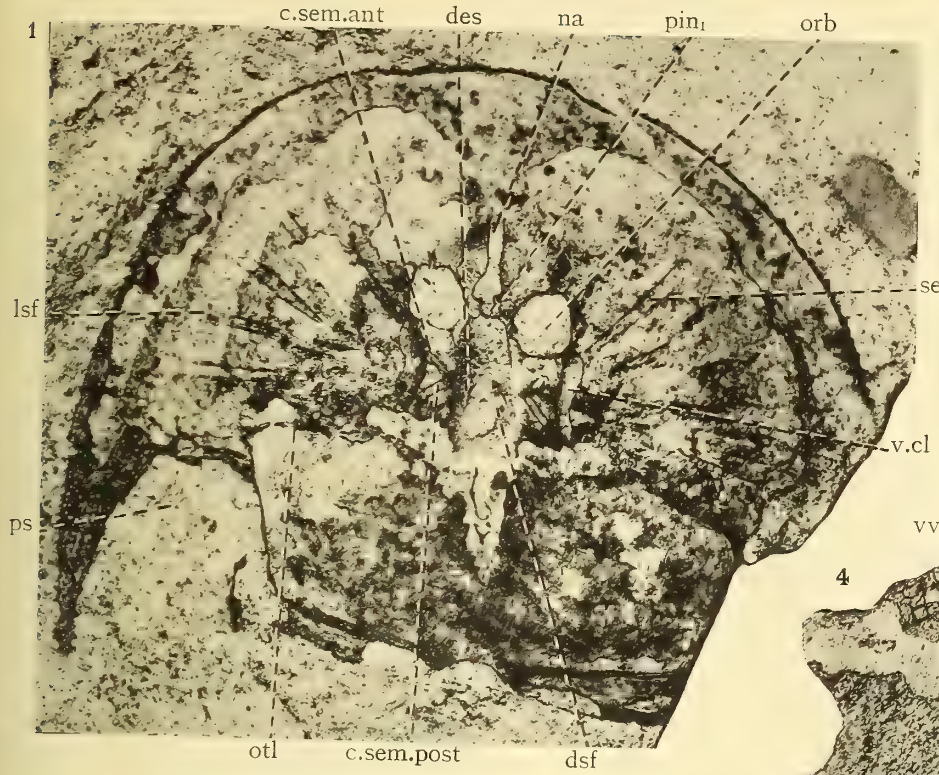

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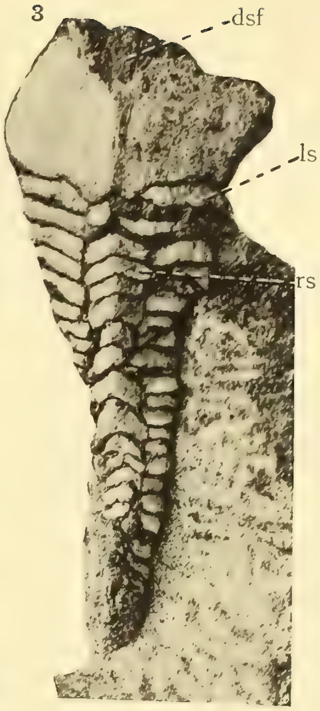

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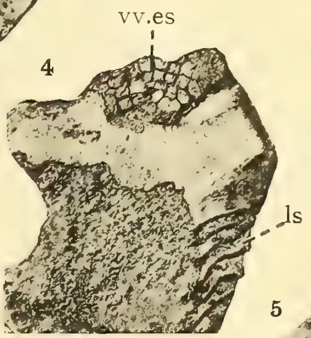

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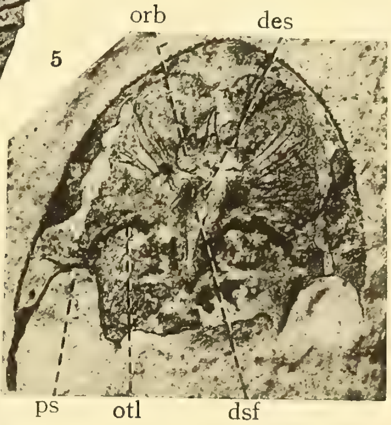

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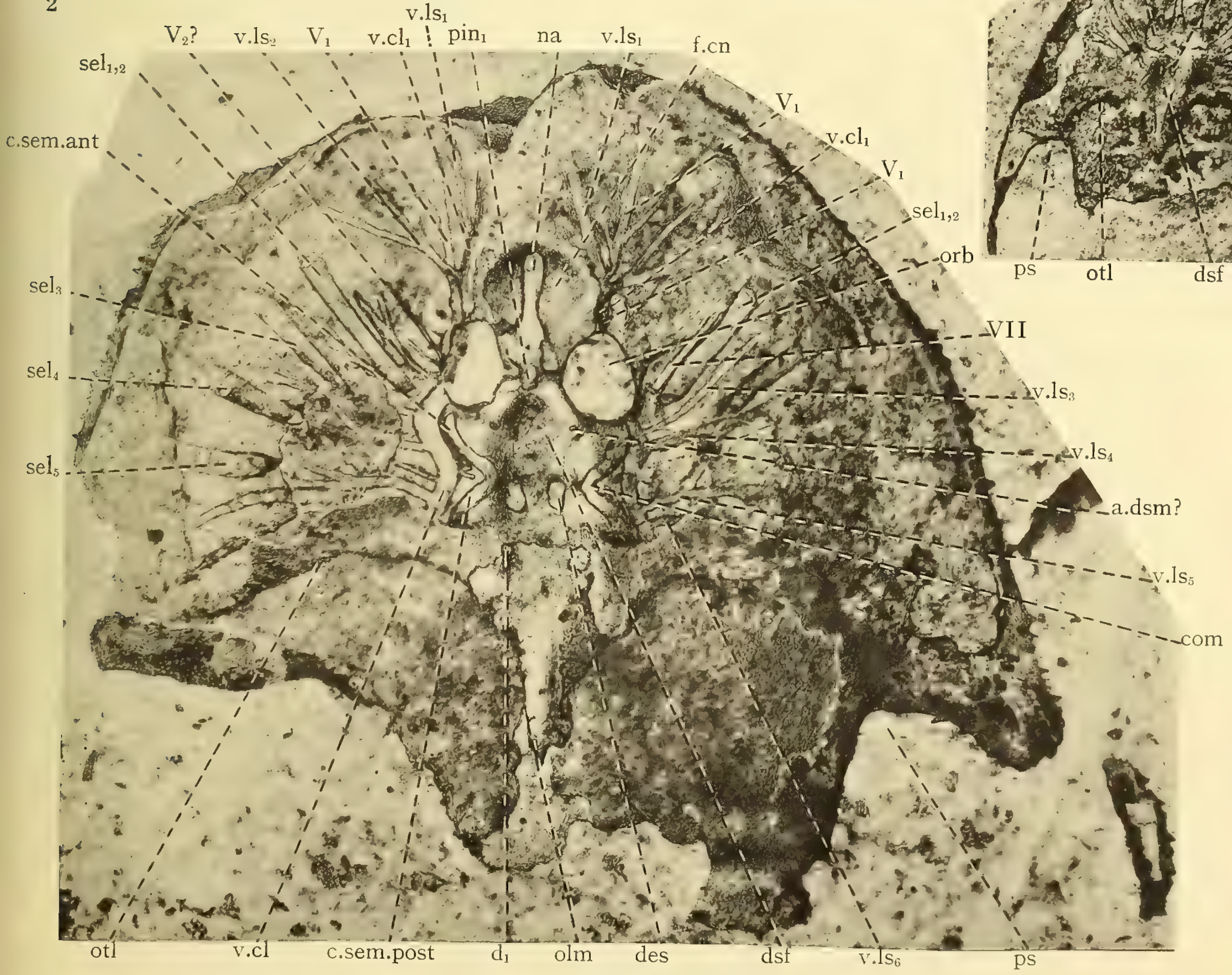

THYESTES

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1 DEC 32
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HISTORY.

PLATE 52.

Sclerodus [Eukeraspis] pustuliferus Agassiz.

FIG. 1.—Dorsal exoskeleton of right half of cephalic shield, preserved mainly as impression of external surface (partial counterpart of specimen in fig. 2). Downtonian (Downton Sandstone): Ludford Lane (Whitcliffe Road), Ludlow, Shropshire. British Museum [no. **45949***b*.—R. Lightbody Bequest, 1874]. × 3 diam.

FIG. 2.—Imperfect cephalic shield, dorsal view. The exoskeleton of the dorsal side is lacking entirely. (Partial counterpart of fig. 1.) British Museum [no. **45949***a*.—R. Lightbody Bequest, 1874]. × 4 diam.

Thyestes egertoni (Lankester).

FIG. 3.—Cephalic shield, dorsal view. The dorsal parts have been removed to show internal structures. Downtonian ("Ludlow Mud"): Ledbury Station, Herefordshire. British Museum [no. **P. 8834.**—G. H. Piper Coll., 1898]. × 2 diam.

FIG. 4.—Cephalic shield, dorsal view. The dorsal parts have been removed, showing a cast of almost the entire oralo-branchial chamber. Downtonian (Mudstone near base of Passage Beds): Ledbury Station, Herefordshire. British Museum [no. **P. 5314.**—G. H. Piper Coll., 1887]. × 2 diam.

Didymaspis grindrodi Lankester.

FIG. 5.—Cephalic shield, dorsal view. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 5313.**—G. H. Piper Coll., 1887]. × 3 diam.

am.ant, division of labyrinth cavity for ampulla anterior; *com*, commissural division of labyrinth cavity; *c.sem.ant*, division of labyrinth cavity for canalis semicircularis anterior; *c.sem.post*, division of labyrinth cavity for canalis semicircularis posterior; *des*, canal of nerve of dorsal electric field; *dsf*, dorsal electric field; *dpr*, supra-oral field; *f.cn*, fossa circum-nasalis; for_1–for_4, marginal fenestrae of cephalic shield; *k*, k_1–k_3, casts of branchial fossae; *lsf*, lateral electric field; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *oes*, opening in post-branchial wall for oesophagus and perhaps also for certain other structures; *olm*, lateral margin of occipital region of endoskeleton; *orb*, orbital opening and cavity; *otl*, posterior margin of endoskeleton of otic region, passing laterally into medial margin of endoskeletal shoulder-girdle, and medially into lateral margin of endoskeleton of occipital region; *pin*, pineal canal; *ps*, pectoral sinus; $sel_{1,2}$, common canal of two most anterior nerves of lateral electric field; sel_3–sel_6, canals of nerves 3–6 of lateral electric field; *tel*, division of cavum cerebrale cranii for telencephalon; *v.cl*, post-orbital division of canal of v. capitis lateralis; V_1, canal of n. profundus (distal part only); V_2, canal of n. trigeminus proper (distal part only); *VII*?, canal probably for n. facialis (from labyrinth cavity to oralo-branchial chamber, distal part only).

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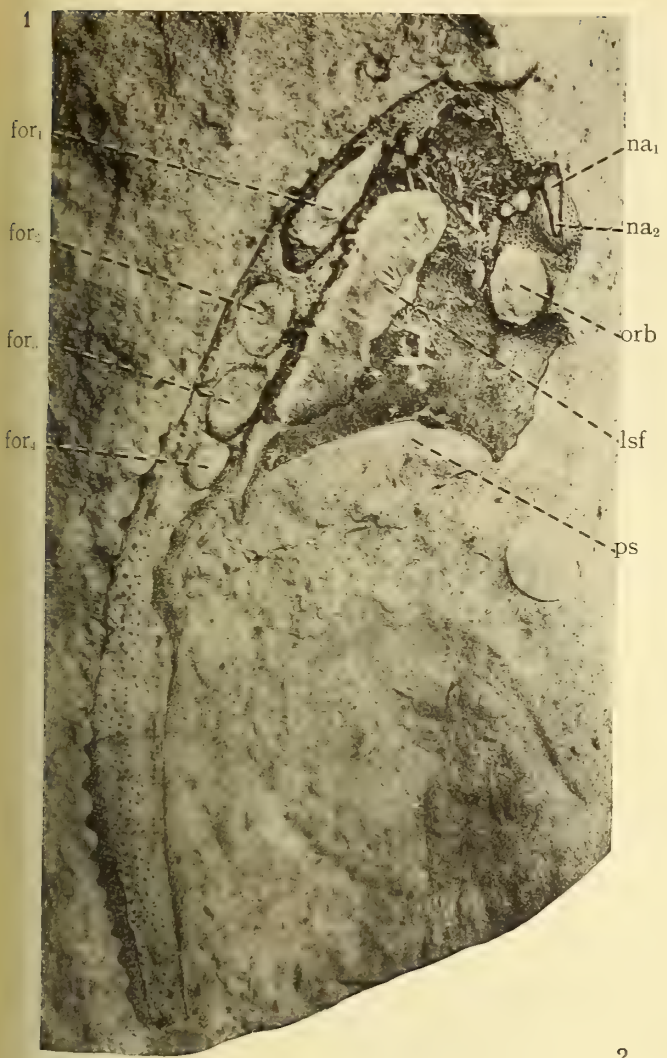

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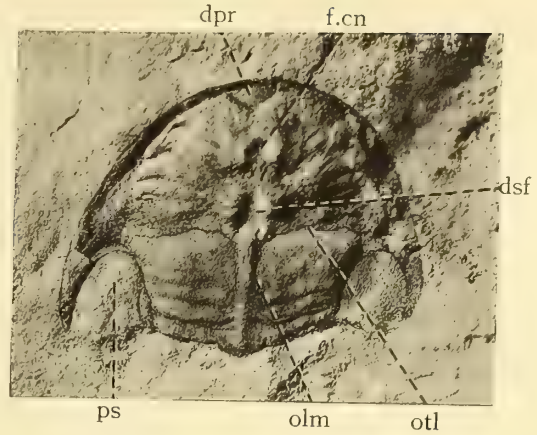

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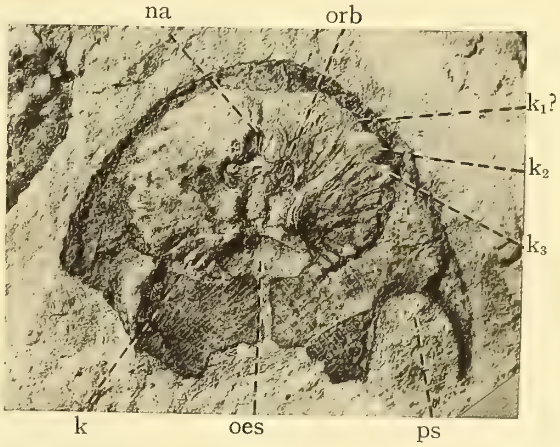

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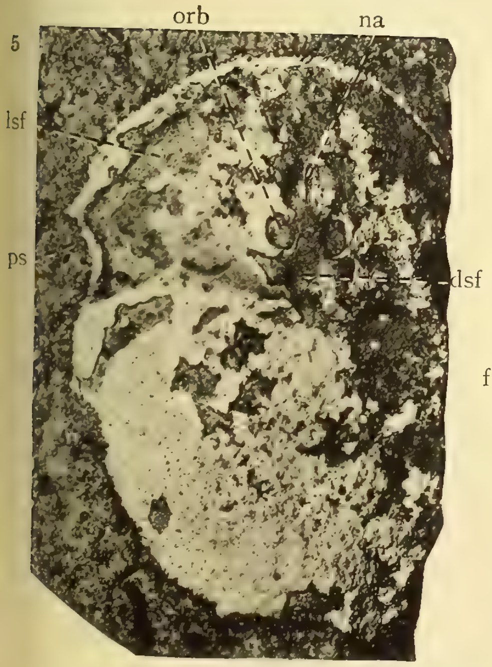

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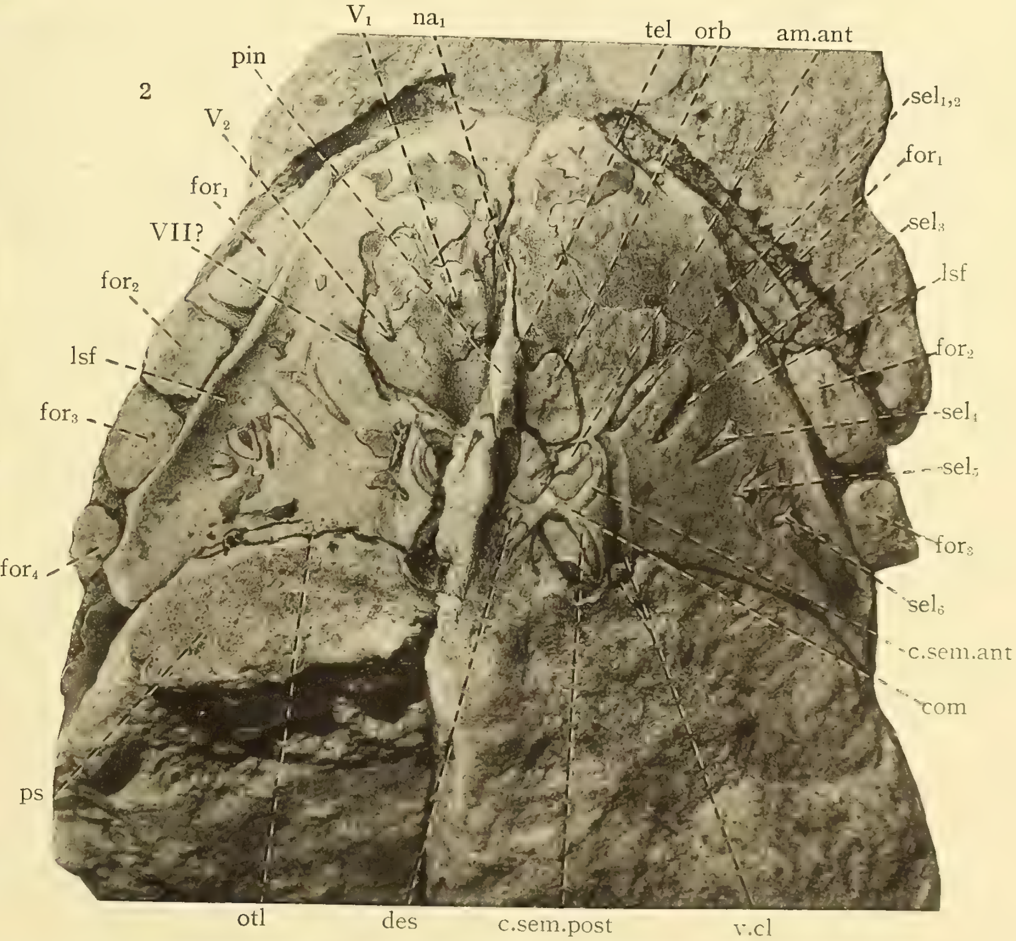

SCLERODUS, THYESTES, and DIDYMASPIS

BRITISH MUSEUM
1 DEC 32
NATURAL HISTORY.

FF

PLATE 53.

Sclerodus [Eukeraspis] pustuliferus Agassiz.

Fig. 1.—Fragment of cornu. Downtonian (Ludlow Bone-bed): Ludlow, Shropshire. British Museum [no. **P. 3247.**—Enniskillen Coll., 1882]. × 3 diam.

Fig. 2.—Fragment of cornu. "Upper Ludlow": Ludford Lane (Whitcliffe Road), near Ludlow, Shropshire. Ludlow Museum [no. **D/g/106***a*.—R. Lightbody Coll.]. × 3 diam.

Fig. 3.—Imperfect cornu. Downtonian ("*Trochus* Bed"): Norton, Shropshire. British Museum [no. **P. 9897.**—W. H. Corfield Coll., 1903]. × 3 diam.

Fig. 4.—Fragment of cornu. Downtonian ("*Trochus* Bed"): Downton Bridge, Herefordshire. British Museum [no. **45970***a*.—R. Lightbody Bequest, 1874]. × 3 diam.

Fig. 5.—Cephalic shield, ventral (internal) view. Downtonian (Downton Sandstone): Ludlow, Shropshire. British Museum [no. **P. 9756.**—G. H. Morton Coll., 1900]. × 3 diam.

Plectrodus sp.

Fig. 6.—Fragment with tooth-like cusps, probably of a jaw. Downtonian (Temeside Shales): Ludlow Station, Shropshire. Ludlow Museum [no. **D/i/34.**—R. Lightbody Coll.]. × 2 diam.

a.car, canal of carotid artery; *aort.gr*, aortic groove; *f.sn*, sub-nasal fossa; for_1–for_4, marginal fenestrae of cephalic shield; *hy.s*, division of ethmoidal and cranial cavities for hypophysial sac; *orb.ot.gr*, orbito-otic groove on roof of oralo-branchial chamber; *p.brw*, post-branchial wall (dorsal part); *pr.au*, otic prominence; *pr.orb*, orbital prominence; *r.aort*, imperfect aortic ridge in ventral view; *VII*, groove for n. facialis after its entrance into oralo-branchial chamber, and foramen through which it entered; *IXa*, opening of n. glossopharyngeus into oralo-branchial chamber.

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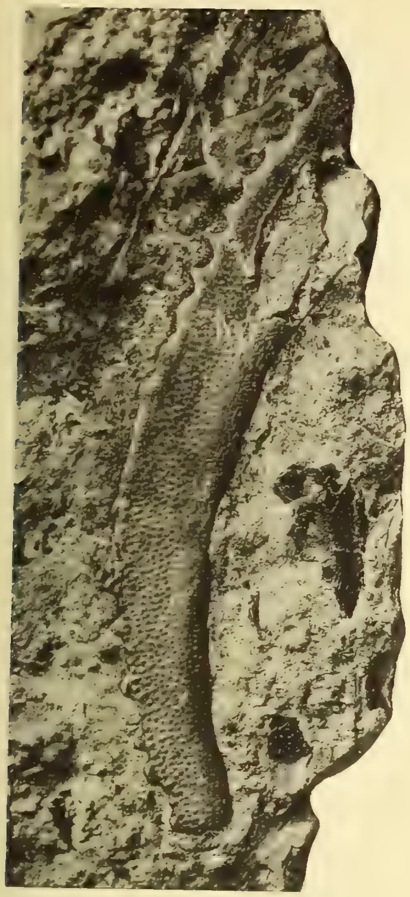

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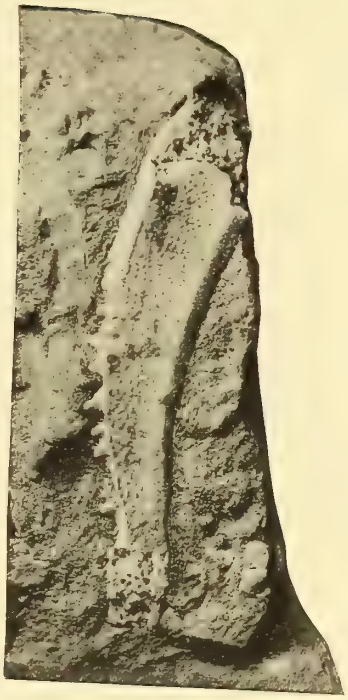

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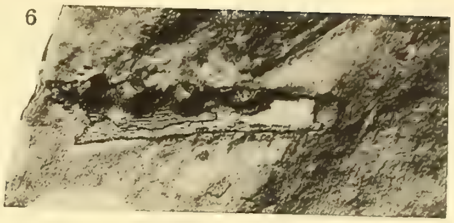

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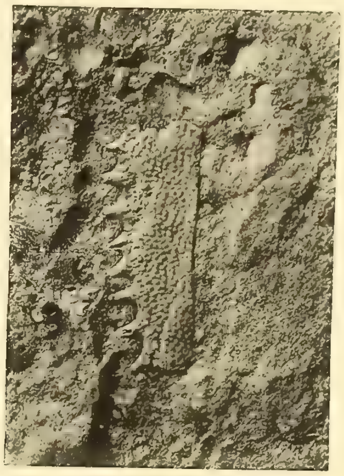

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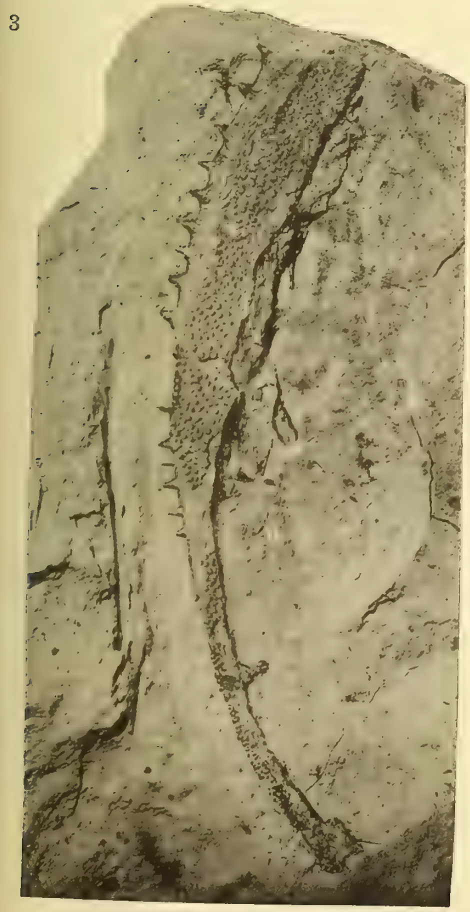

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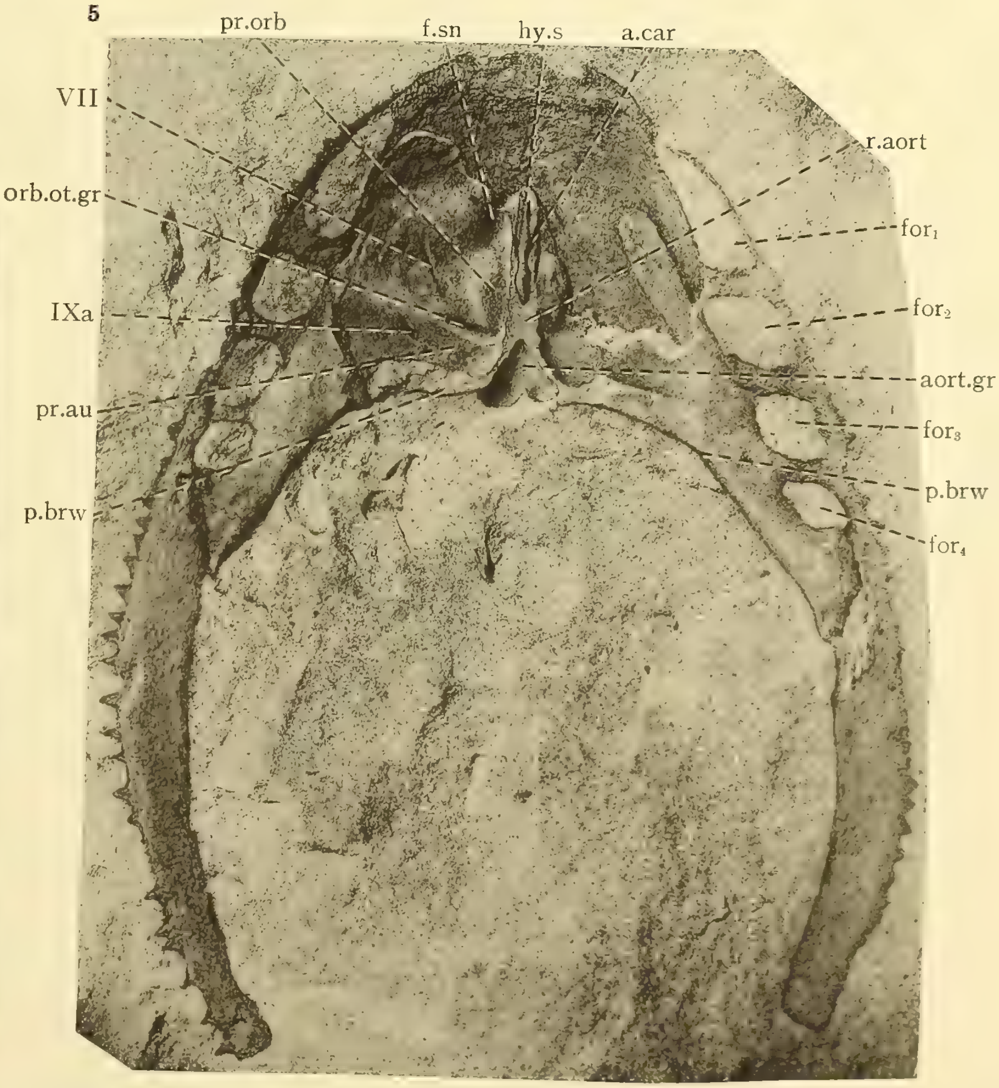

SCLERODUS and PLECTRODUS

BRITISH
MUSEUM
1 DEC 52
NATURAL
HISTORY.

PLATE 54.

Didymaspis grindrodi Lankester.

Fig. 1.—Cephalic shield, dorsal view. The specimen shows parts of the dorsal surface, but chiefly details of the oralo-branchial chamber and an impression of the ventral exoskeleton of the inter-zonal part. Downtonian: Man Brook, Trimpley, Worcestershire. British Museum [no. **P. 16140.**—W. W. King Coll., 1931]. × 3 diam.

Fig. 2.—Anterior part of same specimen. Approx. × 6 diam.

Fig. 3.—Cephalic shield, dorsal view. Over most of the dorsal side of the inter-zonal part the exoskeleton is represented only by an impression of its under-surface. Downtonian: Man Brook, Trimpley, Worcestershire. British Museum [no. **P. 16141.**—W. W. King Coll., 1931]. × 3 diam.

Fig. 4.—Cephalic shield, dorsal view. Almost the entire dorsal exoskeleton is wanting. (Same specimen as in Pl. 45, fig. 1.) × ⟨ 3 diam.

a.gr, cast of aortic groove on under-surface of exoskeleton. *c.sem.ant*, *c.sem.post*, divisions of labyrinth cavity of anterior and posterior semicircular canals respectively; d_1, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *des*, canal of nerve of dorsal electric field; *dsf*, dorsal electric field; *dpr*, impression of supra-oral field; k_1–k_{10}, casts of branchial fossae 1–10; *lsf*, lateral electric field; *med*, division of cavum cerebrale cranii for medulla oblongata; *na*, naso-hypophysial aperture; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *olm*, lateral margin of occipital region of endoskeleton (perichondrial bone-layer of external surface); *orb*, orbital opening; *otl*, posterior margin of endoskeleton of otic region passing laterally into medial margin of endoskeletal shoulder-girdle, and medially into lateral margin of endoskeleton of occipital region; pin_1, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps*, pectoral sinus; *r.pm*, impression of pre-branchial ridge; *sel*, canals of nerves of lateral electric field; $sel_{1,2}$, common canal of two most anterior nerves of lateral electric field; sel_3, canal of third nerve of lateral electric field; *tel*, division of cavum cerebrale cranii for telencephalon; *vc*, ventro-lateral ridge of inter-zonal part; *v.cl*, post-orbital division of canal of v. capitis lateralis; *x*, canal of doubtful origin.

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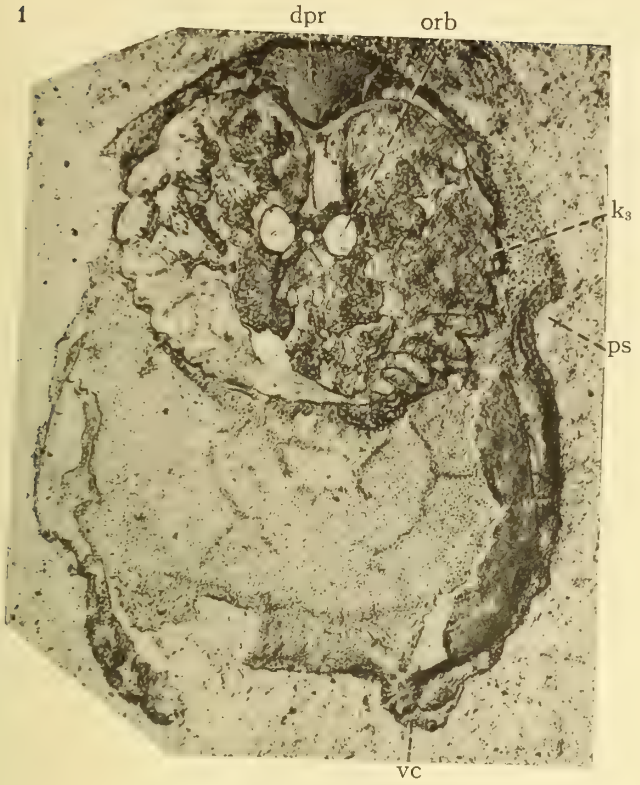

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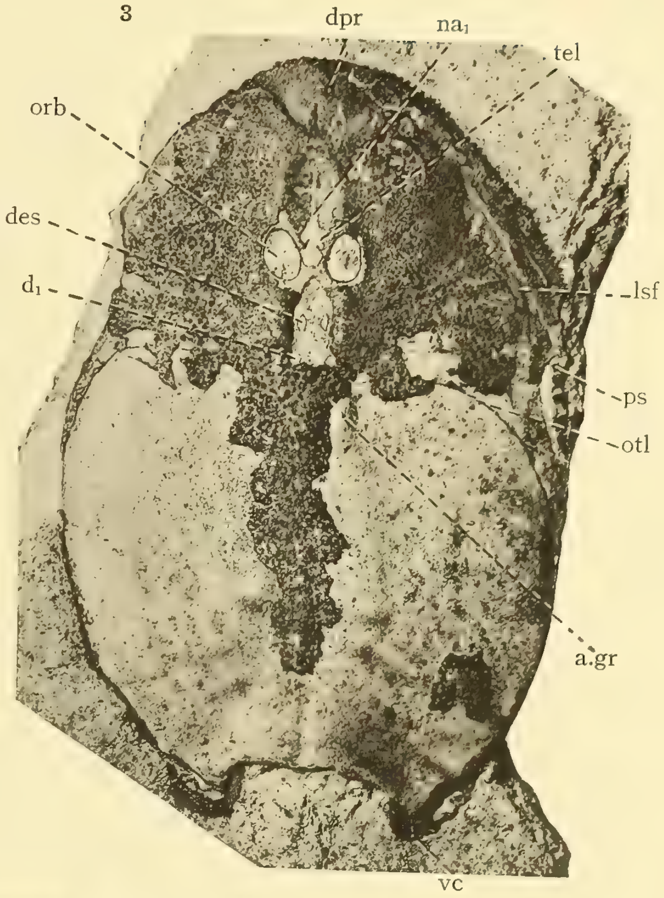

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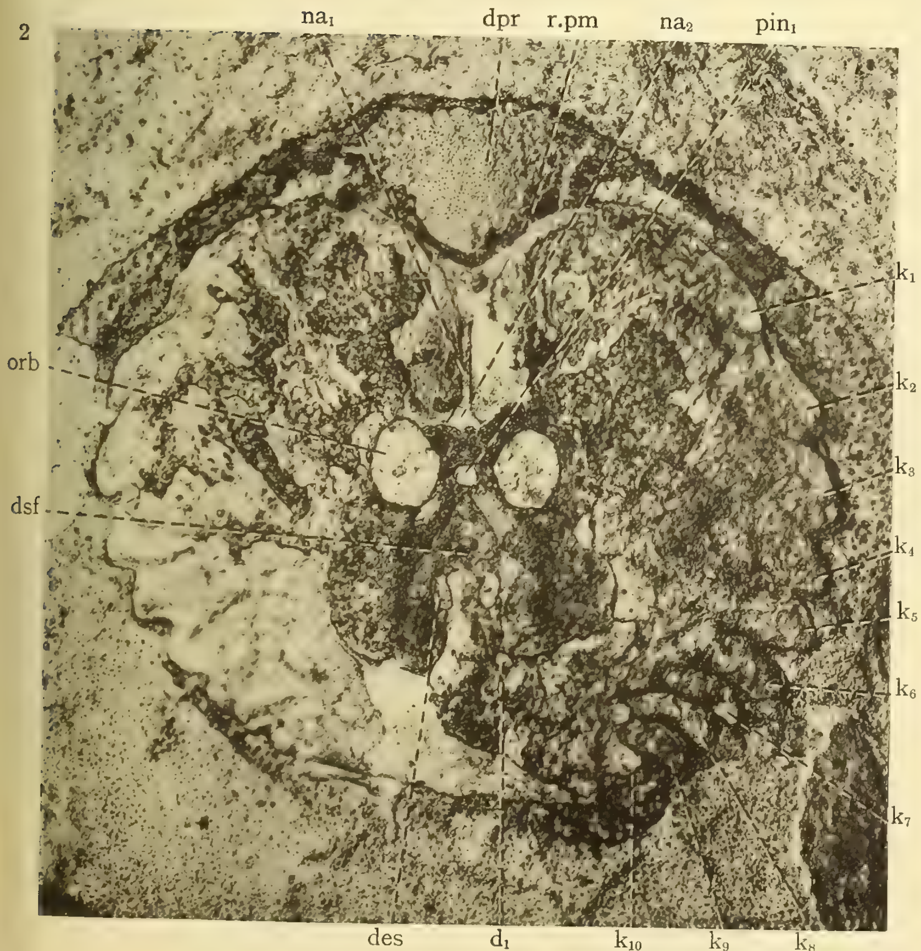

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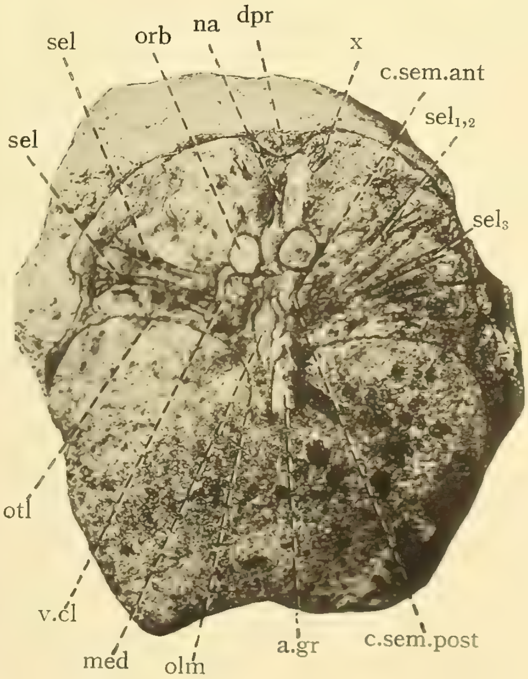

DIDYMASPIS

BRITISH
MUSEUM
1 DEC 52
NATURAL
HISTORY.

PLATE 55.

Didymaspis grindrodi Lankester.

FIG. 1.—Cephalic shield, dorsal view. The dorsal exoskeleton is represented either by an impression of its under-surface or not at all. Downtonian: Man Brook, Trimpley, Worcestershire. British Museum [no. **P. 16142.**—W. W. King Coll., 1931]. × 3 diam.

FIG. 2.—Ventral exoskeleton of imperfect cephalic shield, dorsal (internal) view. "Lower Old Red Sandstone" *: Bush Pitch, near Ledbury, Herefordshire. British Museum [no. **P. 5043.**—J. E. Lee Coll., 1885]. × 4 diam.

FIG. 3.—Cephalic shield showing partly an internal view of the dorsal exoskeleton, and partly a mould of its outer surface. (See also fig. 4.) Downtonian: Man Brook, Trimpley, Worcestershire. British Museum [no. **P. 12659.**—W. W. King Coll., 1921]. × $4\frac{1}{2}$ diam.

FIG. 4.—Counterpart of specimen in fig. 3, showing portions of the external surface of the dorsal exoskeleton, but mostly an impression of the internal (basal) surface. × 3 diam.

a.gr, cast of aortic groove at side of most posterior part of occipital region of endoskeleton; d_1, canal probably for vein from dorsal electric field, and perhaps also for ductus endolymphaticus; *des*, canal of nerve of dorsal electric field; *dsf*, dorsal electric field; *dpr*, supra-oral field; *ifc*, infra-orbital sensory canal groove; ifc_1, sensory canal groove, which probably corresponds to supra-orbital sensory canal of fishes; *k*, branchial fossae; *lsf*, lateral electric field; na_1, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); na_2, posterior division of naso-hypophysial aperture (nasal opening proper); *obr.f*, oralo-branchial fenestra; *olm*, lateral margin of occipital region of endoskeleton (perichondrial bone-layer of external side); *orb*, orbital opening or cavity; *otl*, posterior margin of endoskeleton of otic region, passing laterally into medial margin of endoskeletal shoulder-girdle, and medially into lateral margin (*olm*) of occipital region; *pin*, pin_1, pineal opening; *ps*, pectoral sinus; $sel_{1,\,2}$, common canal of two most anterior nerves of lateral electric field; sel_5, sel_6, canals of nerves 5 and 6 of lateral electric field; *tel*, division of cavum cerebrale cranii for telencephalon; *vc*, ventro-lateral ridge of inter-zonal part of cephalic shield; *v.cl*, canal of post-orbital division of v. capitis lateralis.

* See p. 200.

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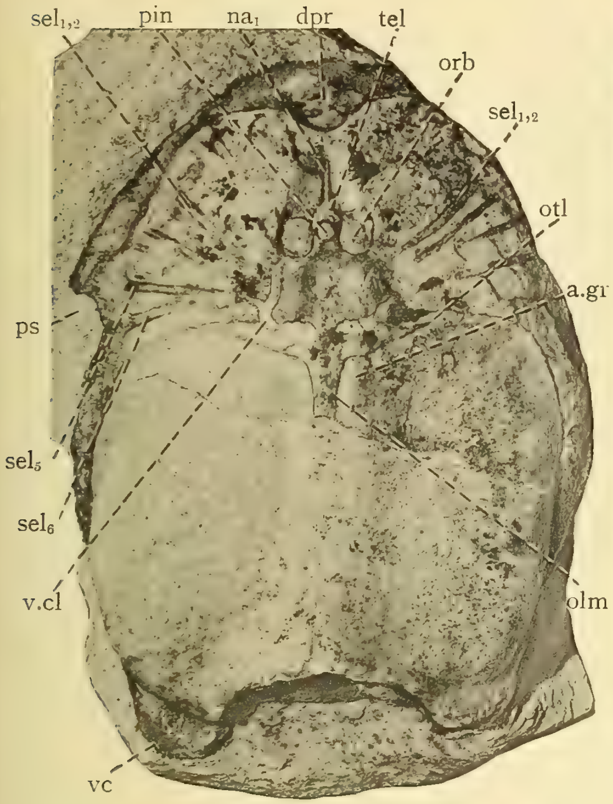

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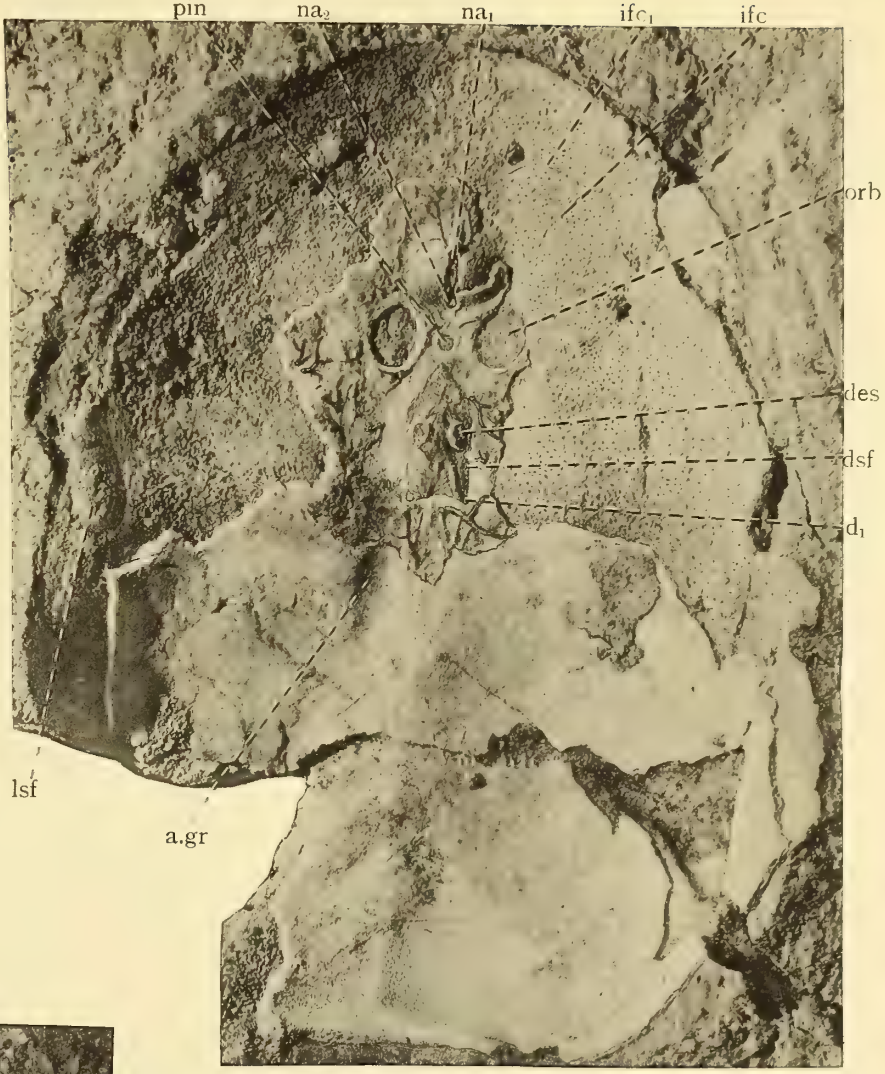

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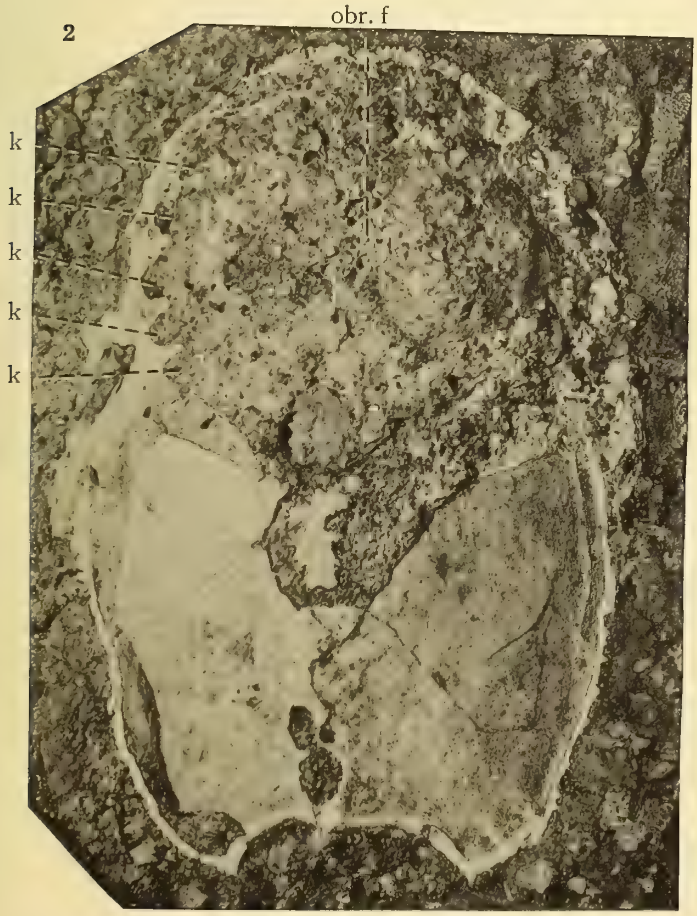

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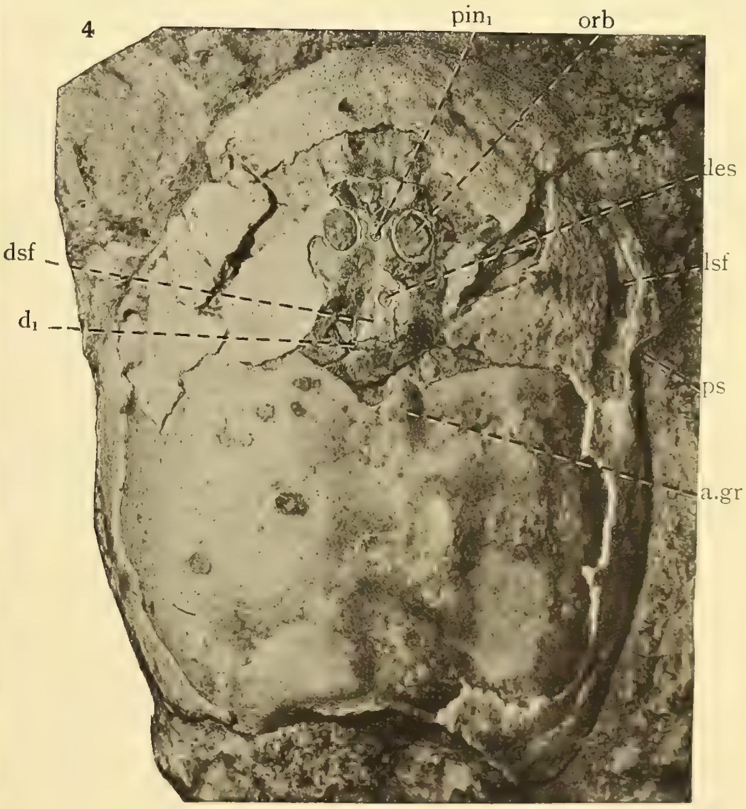

DIDYMASPIS

BRITISH MUSEUM
1 DEC 32
NATURAL HISTORY

PLATE 56.

Sclerodus [Eukeraspis] pustuliferus Agassiz.

Fig. 1.—Section through a cornu. Inner margin on the left. Downtonian (Downton Sandstone): Ludford Lane (Whitcliffe Road), near Ludlow, Shropshire. British Museum [no. **45973.**—R. Lightbody Bequest, 1874]. Approx. × 20 diam.

Cephalaspis lankesteri, sp. nov.

Fig. 2.—Mucous canal system in part of dorsal exoskeleton of cephalic shield, ventral view. The basal layer has been entirely removed. (Same specimen, the Holotype, as in Pl. 17, fig. 3.) Approx. × 15 diam.

Cephalaspis sp.

Fig. 3.—Mucous canal system in part of dorsal exoskeleton of cephalic shield, situated rostrally to the naso-hypophysial aperture, ventral view. The basal layer of the exoskeleton has been removed. (Same specimen as in Pl. 23, fig. 1.) Approx. × 12 diam.

iac, inter-areal mucous canals; *ita*, intra-areal mucous canals; *lsf*, lateral electric field (rostral end); *mc*, mucous canals in general; *ml*, middle layer of exoskeleton (basal part with radiating canals only shown); *p*, pores of mucous canals (in superficial layer); *rad.c*, radiating canals; *sl*, superficial layer (with pores but without mucous canals).

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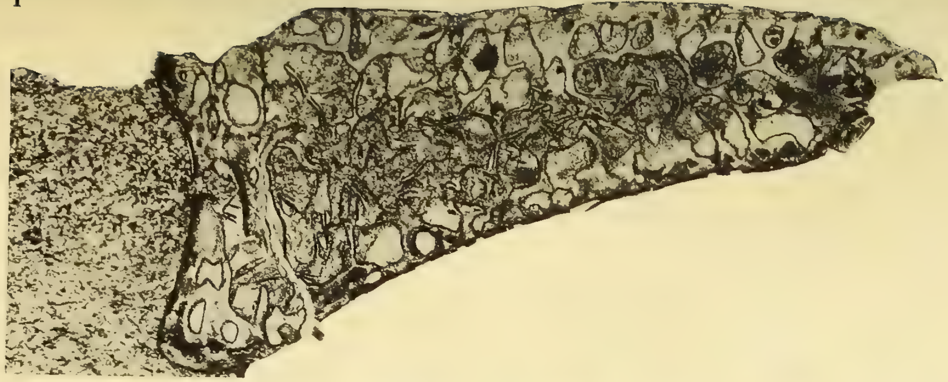

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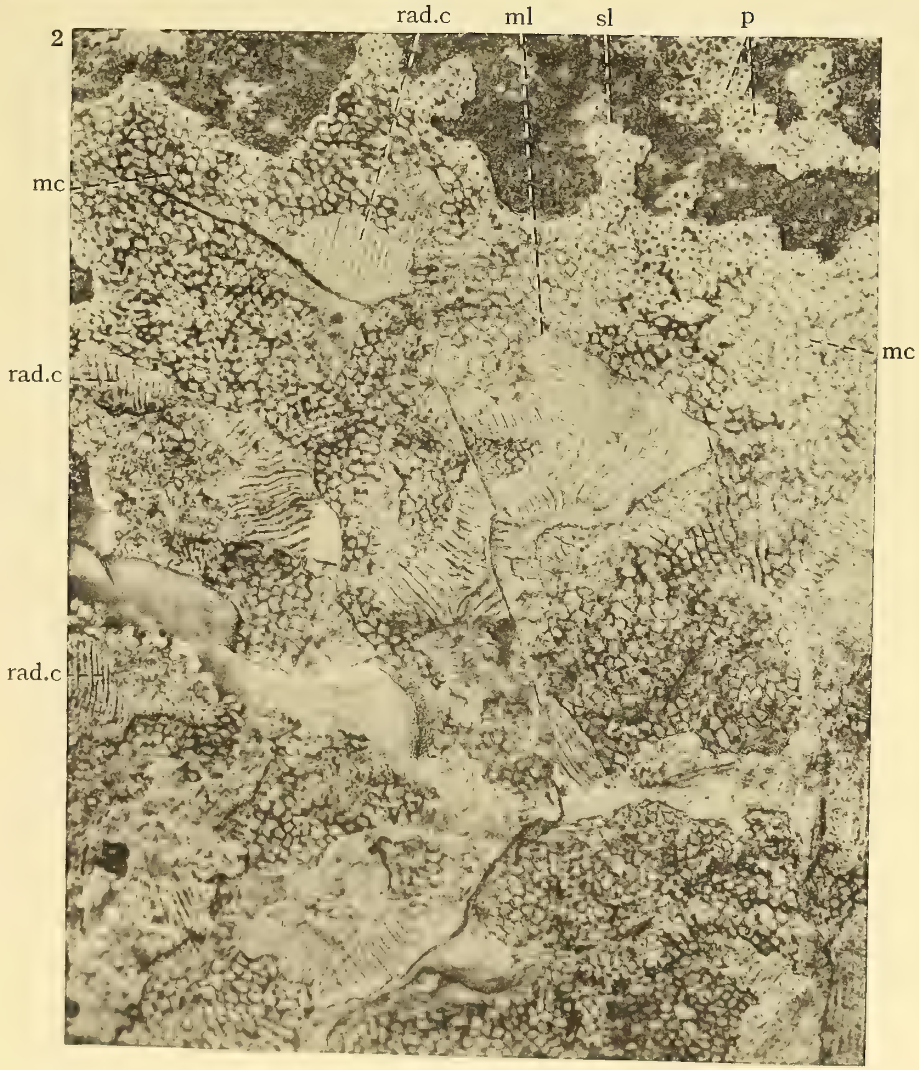

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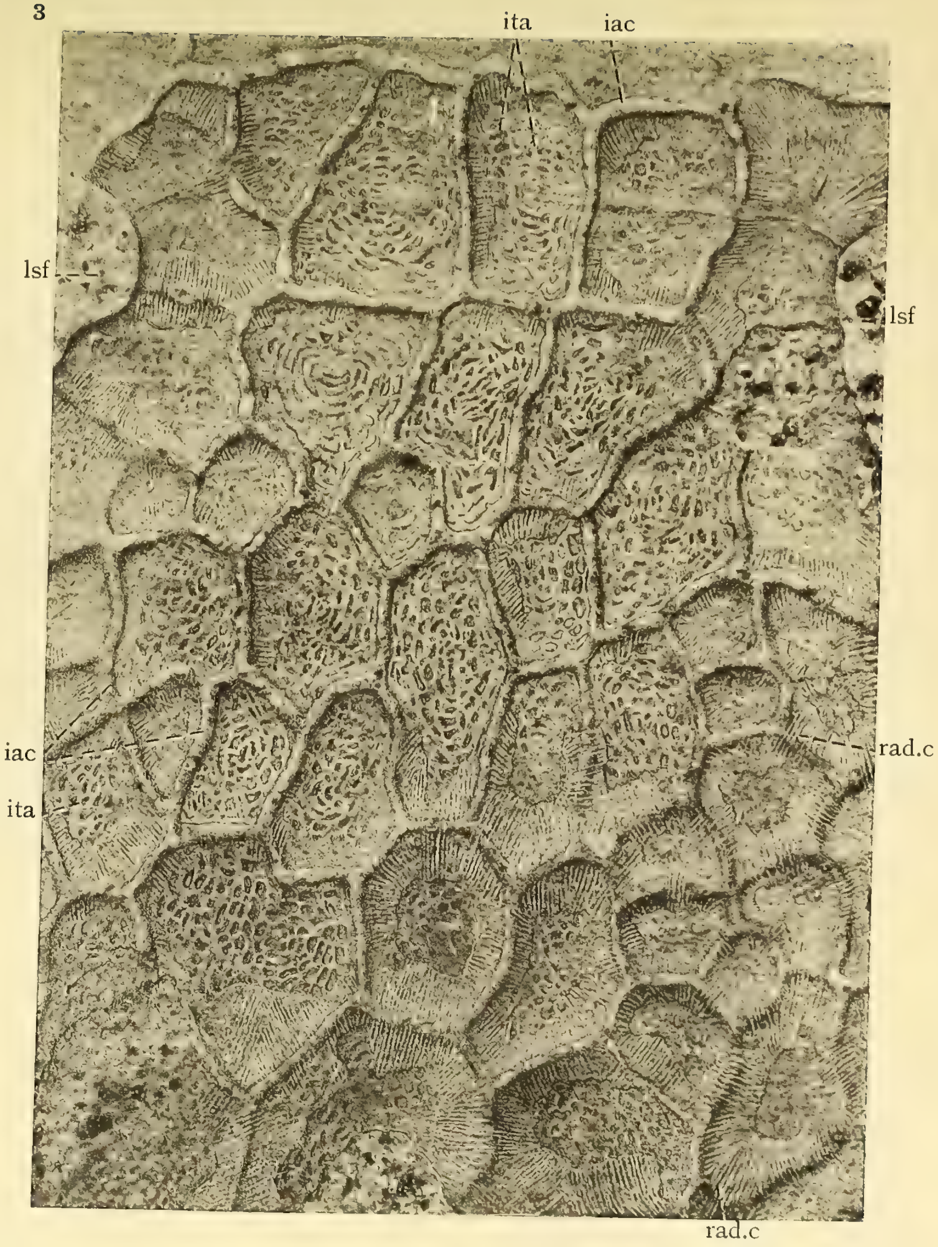

SCLERODUS and CEPHALASPIS

BRITISH
MUSEUM
1 DEC 32
NATURAL
HISTORY.

GG

PLATE 57.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Part of squamation of right side of body immediately behind cephalic shield. The scales are seen from the medial (inner) side, and the basal layer having been largely removed, the base of the middle layer is well exposed. In places the middle layer is also absent, so that the superficial layer is shown. Downtonian: Ledbury Station, Herefordshire. British Museum [no. **P. 8802.**—G. H. Piper Coll., 1898]. Approx. × 10 diam.

FIG. 2.—Section through superficial parts of exoskeleton. The relations of the external branches of the radiating canals are well displayed. Downtonian: loc. uncertain. British Museum [no. **P. 14012.**—History unknown]. × 240 diam.

FIG. 3.—Part of dorsal exoskeleton of cephalic shield, dorsal view. The superficial layer is wanting in places, so that the arrangement of the mucous canal system can be seen. (Same specimen as in Pl. 1, figs. 1–3; Pl. 2, fig. 1.) Approx. × 15 diam.

c.asc, ascending vascular canals of basal layer (most distal parts only preserved); *ceph*, posterior part of cephalic shield; *ebc*, external branches of radiating canals; *iac*, inter-areal mucous canals; *ita*, intra-areal mucous canals; ls_1–ls_5, lateral scales of transverse rows 1–5 behind cephalic shield; *ml*, middle layer of exoskeleton; *p*, pores of mucous canal system in superficial layer; *rad.c*, radiating canals; *sl*, superficial layer of exoskeleton.

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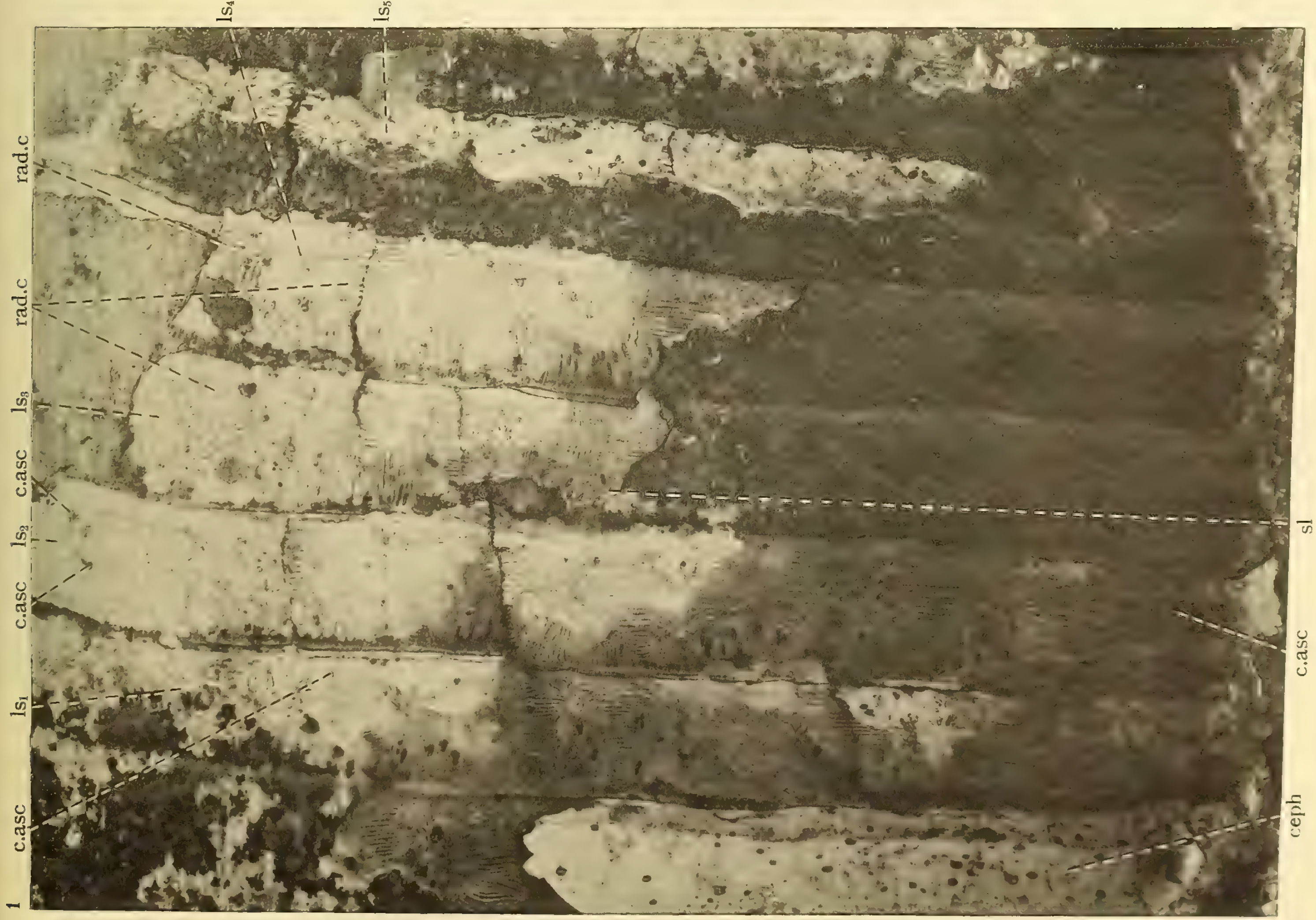

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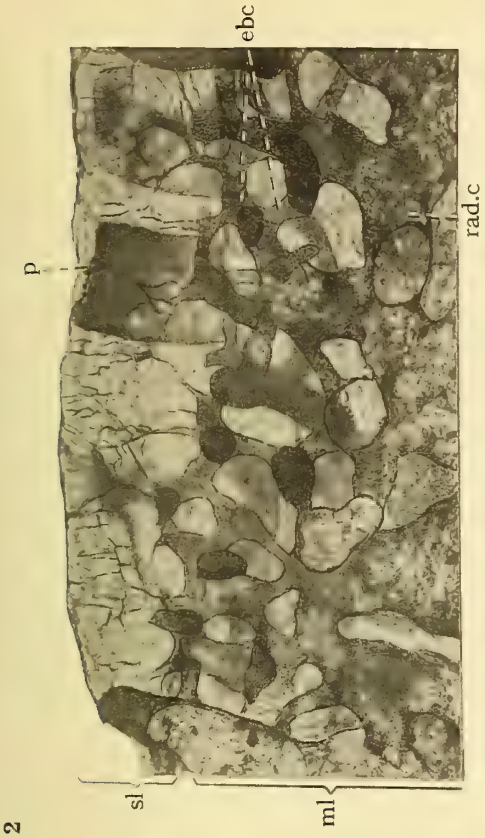

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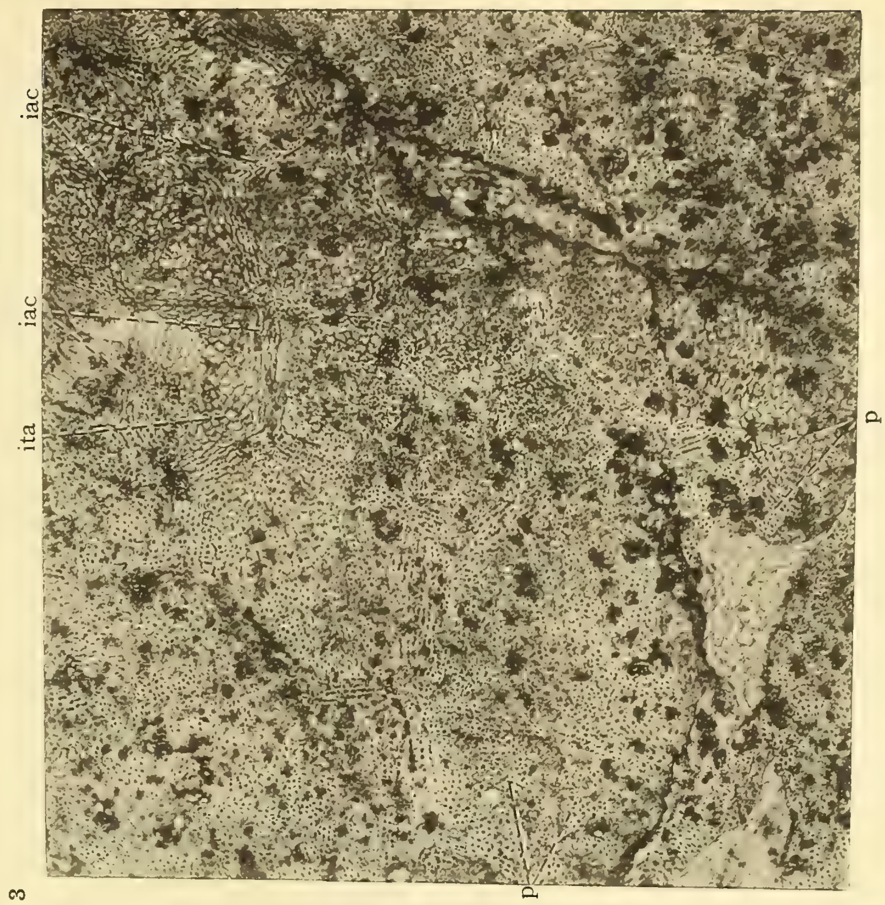


HEMICYCLASPIS

BRITISH
MUSEUM
1 DEC 32
NATURAL
HISTORY.

PLATE 58.

Cephalaspis powriei Lankester, var. *asper* Lankester.

FIG. 1.—Tubercular ornamentation on posterior part of dorsal side of cephalic shield doubtfully referred to this variety. Lower Old Red Sandstone : Turin Hill, Forfarshire. Royal Scottish Museum, Edinburgh [no. **1891.92.169**]. Approx. × 5 diam.

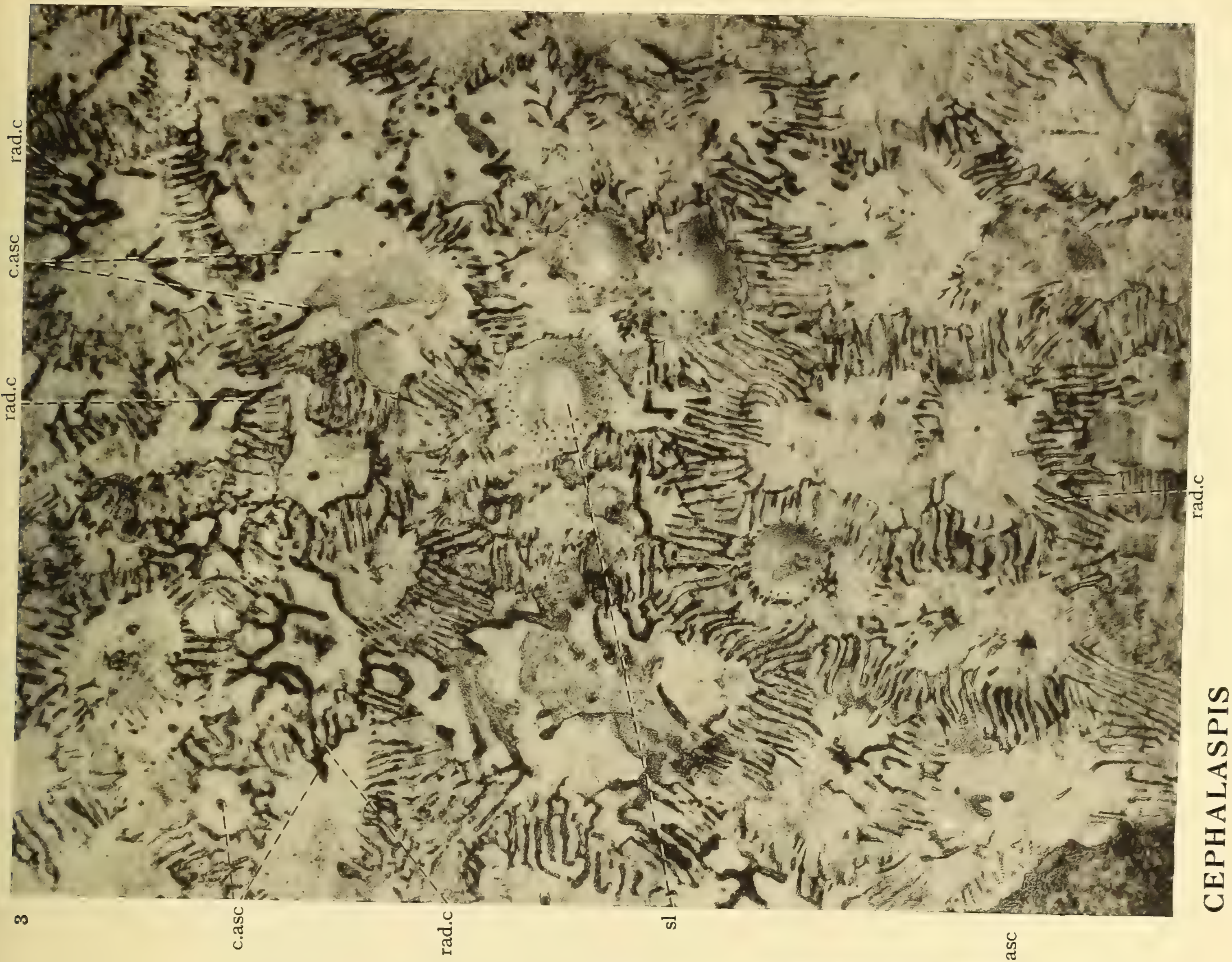
Cephalaspis powriei Lankester, var. *brevicornis* nov.

FIG. 2.—Section through dorsal exoskeleton of cephalic shield parallel to basal surface. The position of the venous ring-sinuses in the basal layer and their relations to the radiating canals are shown. Lower Old Red Sandstone : Rossie Priory, Perthshire. Museum of Practical Geology, London [no. **47787.**—Kinnaird Coll.]. Approx. × 12 diam.

Cephalaspis salweyi Egerton.

FIG. 3.—Part of dorsal exoskeleton of cephalic shield, dorsal view. The external parts (the tubercles and much of the middle layer) are to a great extent missing. (Same specimen as in Pl. 12, fig. 1.) Approx. × 20 diam.

c.asc, ascending vascular canals; *c.des*, descending vascular canals; *rad.c.* radiating canals; *r.sin*, venous ring-sinus (more or less imperfectly developed); *sl*, superficial layer (in tubercles forming ornamentation).



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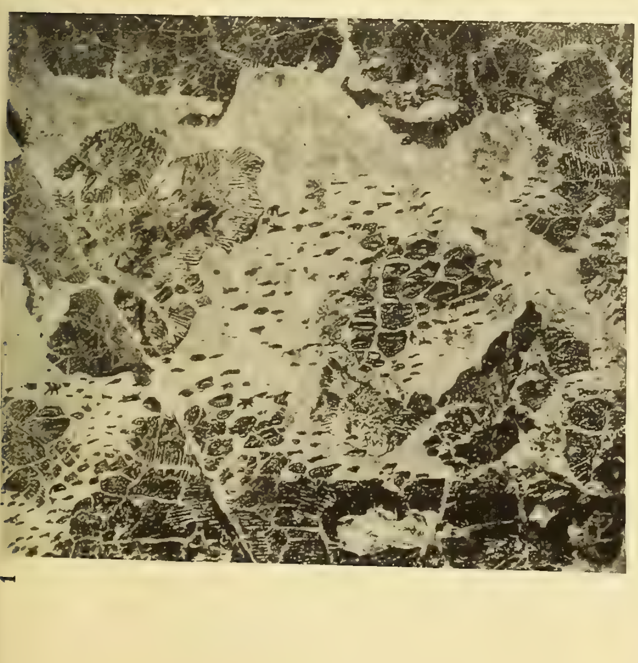

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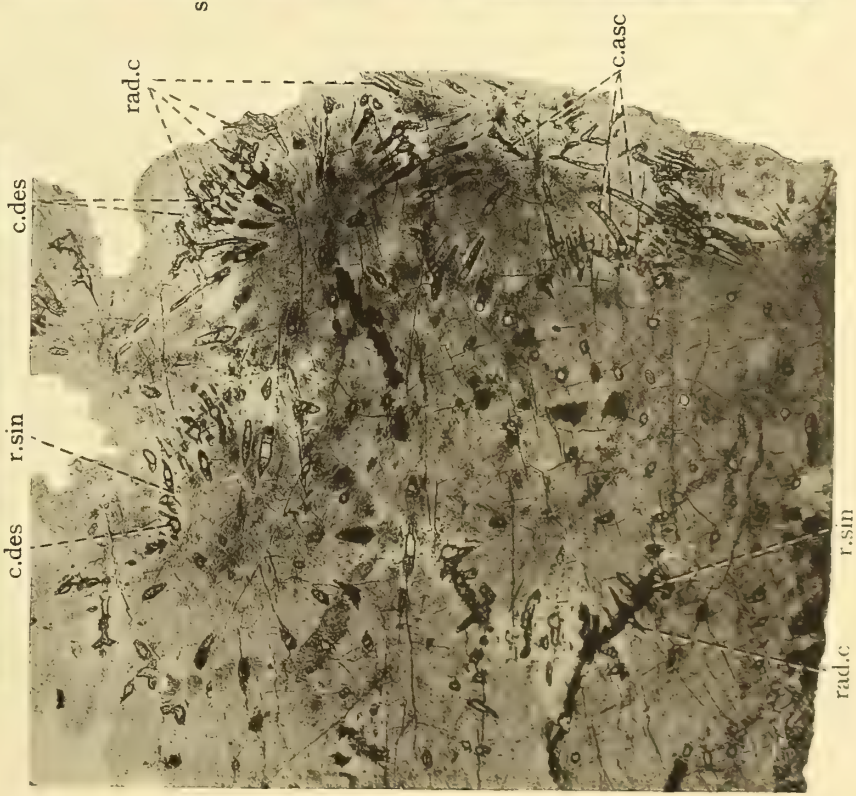

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CEPHALASPIS

BRITISH MUSEUM
1 DEC 32
NATURAL HISTORY

PLATE 59.

Cephalaspis pagei Lankester.

Fig. 1.—Cephalic shield doubtfully referred to this species, lateral view. (Same specimen as in Pl. 23, fig. 2.) Nat. size.

Cephalaspis fletti, sp. nov.

Fig. 2.—Imperfect cephalic shield doubtfully referred to this species, dorsal view. The shield has been sectioned transversely. Lower Old Red Sandstone : Cradley, Herefordshire. British Museum [no. **P. 3235.**—Enniskillen Coll., 1882]. Approx. × 1½ diam.

Cephalaspis sp.

Fig. 3.—Section through exoskeleton of cephalic shield showing position of mucous canal system. The superficial layer in this species forms a continuous covering to the middle layer. (Same specimen as in Pl. 45, fig. 3 : see also Pl. 64, figs. 2, 3.)

Cephalaspis salweyi Egerton.

Figs. 4, 5.—Sections through most basal parts of basal layer of dorsal exoskeleton of cephalic shield, showing position and relations of venous ring-sinuses. The sections are made almost parallel with the under-surface of the basal layer. Lower Old Red Sandstone : loc. uncertain. British Museum [no. **35499.**—Purchased, 1860]. Approx. × 12 diam.

a, areas where descending branches from radiating canals reached and opened into venous ring-sinuses (removed by grinding) ; *bl*, basal layer of exoskeleton ; *c.asc*, ascending vascular canals ; *ebc*, external branches of radiating canals ; *iac*, inter-areal mucous canals ; *ita*, intra-areal mucous canals ; *ml*, middle layer of exoskeleton ; *rad.c*, radiating canals ; *r.sin*, venous ring-sinus (not completely closed but forming grooves on under-surface of basal layer) ; *sl*, superficial layer of exoskeleton.

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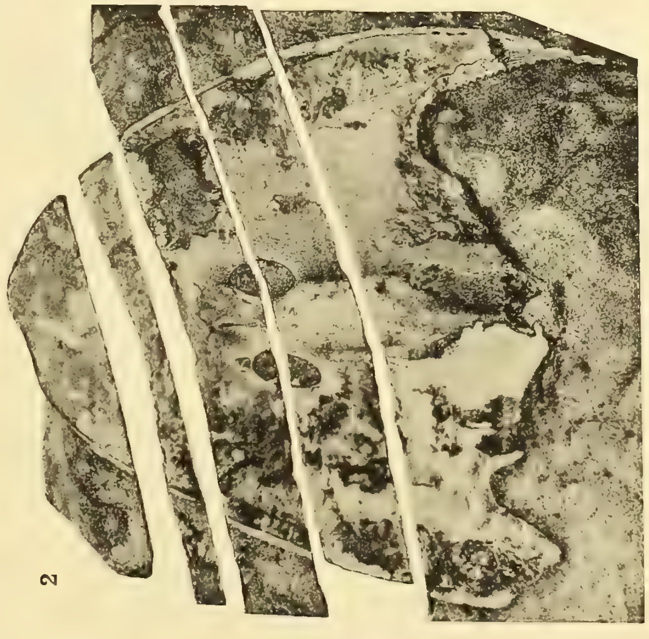

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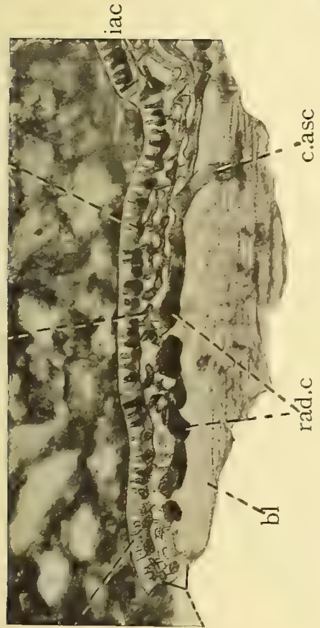

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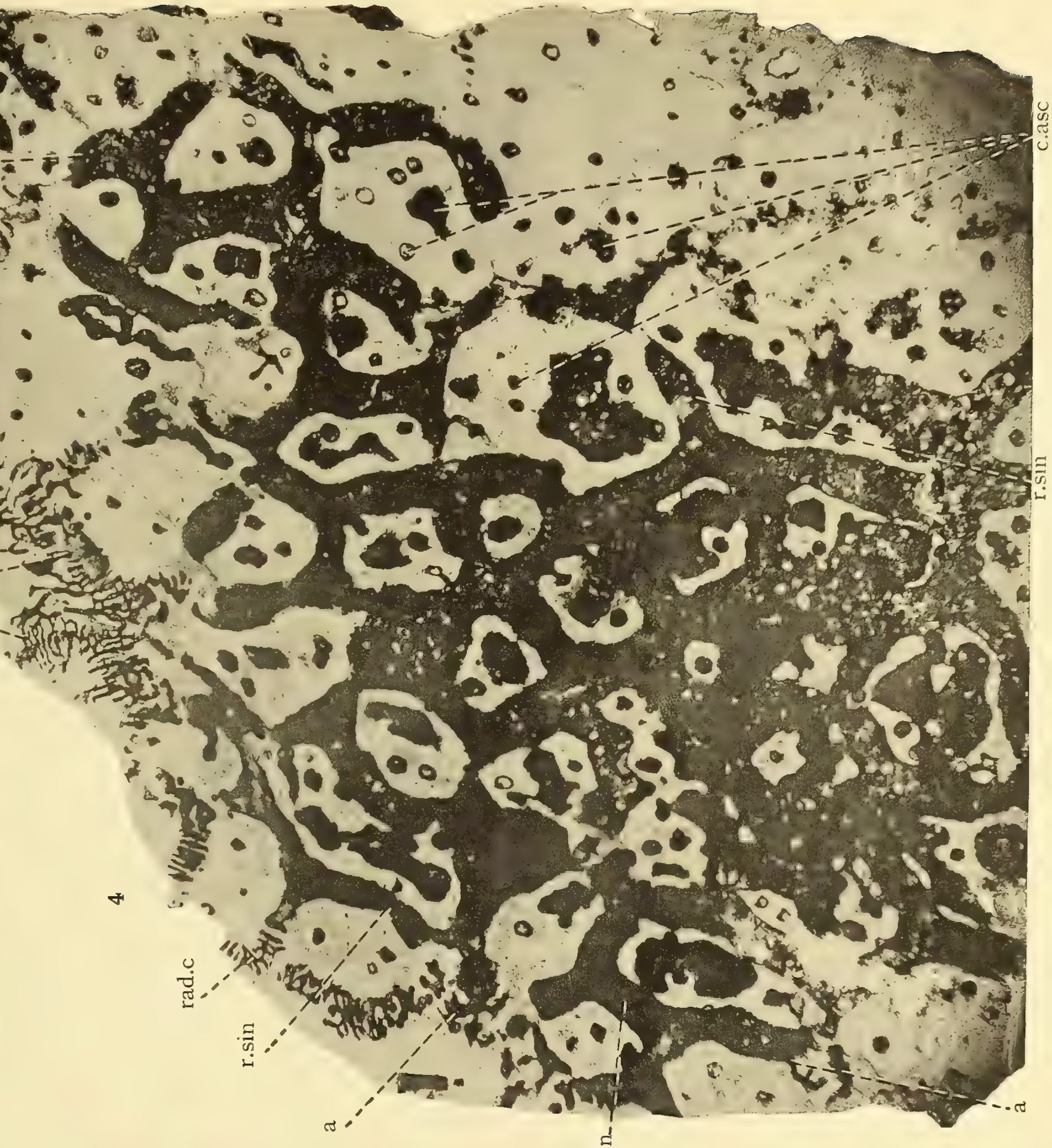

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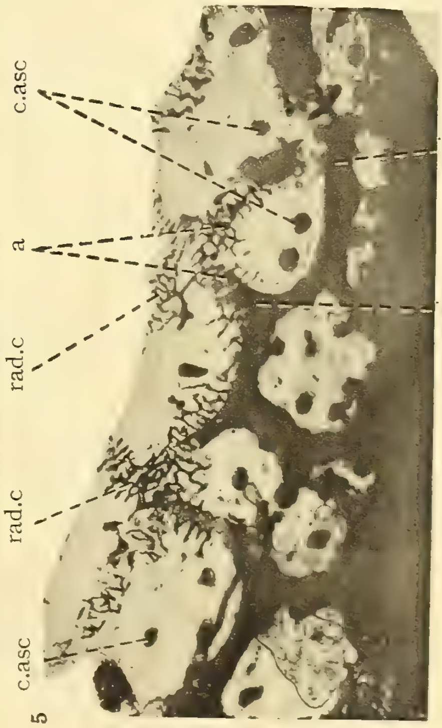

CEPHALASPIS

BRITISH
MUSEUM

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NATURAL
HISTORY.

PLATE 60.

Hemicyclaspis murchisoni (Egerton).

FIGS. 1–4.—Transverse sections through dorsal exoskeleton of cephalic shield. All the sections are taken close to the rostral margin of the shield, and in consequence the middle layer is very thick. The mucous canals are filled by a darker matrix than the other canals. (See also Pl. 64, fig. 1; Pl. 65, fig. 1.) Lower Old Red Sandstone: loc. uncertain. British Museum [no. **P. 14012.**—History unknown].

(Fig. 1.) Section through entire exoskeleton. Approx. × 55 diam.

(Fig. 2.) Section through superficial layer and part of middle layer. Approx. × 105 diam.

(Fig. 3.) Part of same section more highly magnified to show detailed arrangement and relations of external branches of radiating canals. Approx. × 240 diam.

(Fig. 4.) Section showing similar details. Approx. × 240 diam.

bl, basal layer; *ebc*, external branches of radiating canals (their continuity in the fossil condition with the dentine-canals of the superficial layer is well displayed); *mc*, mucous canals; *ml*, middle layer of exoskeleton; *p*, pores of mucous canals; *rad.c*, radiating canals; *sl*, superficial layer of exoskeleton.

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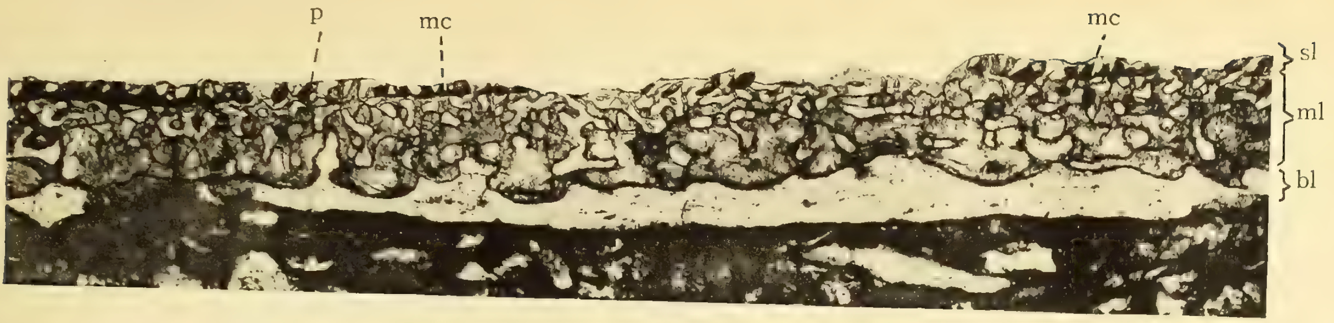

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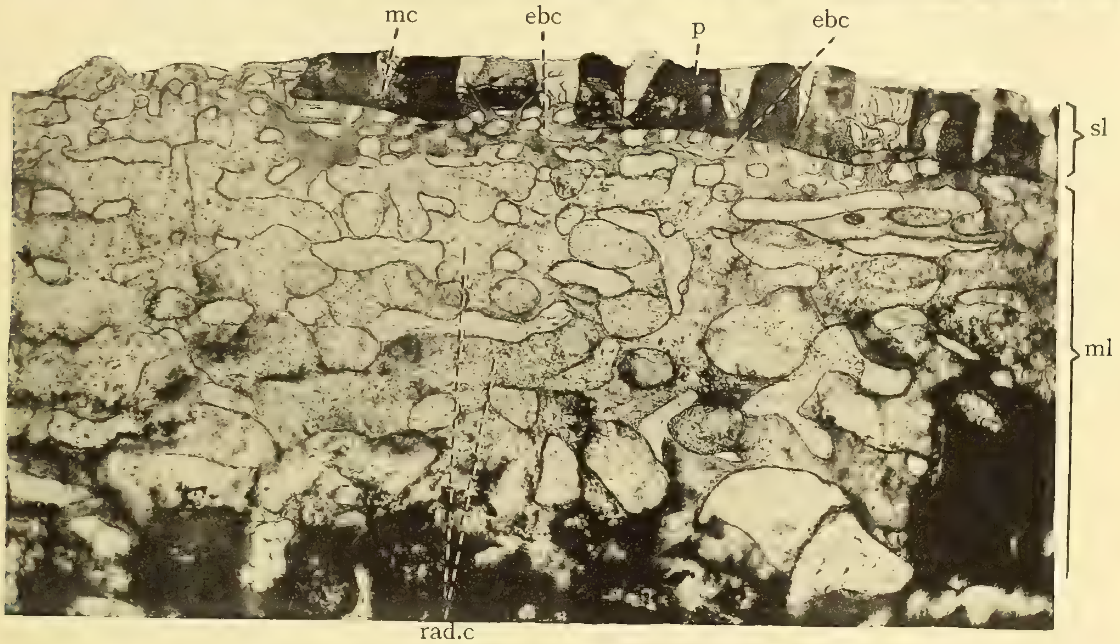

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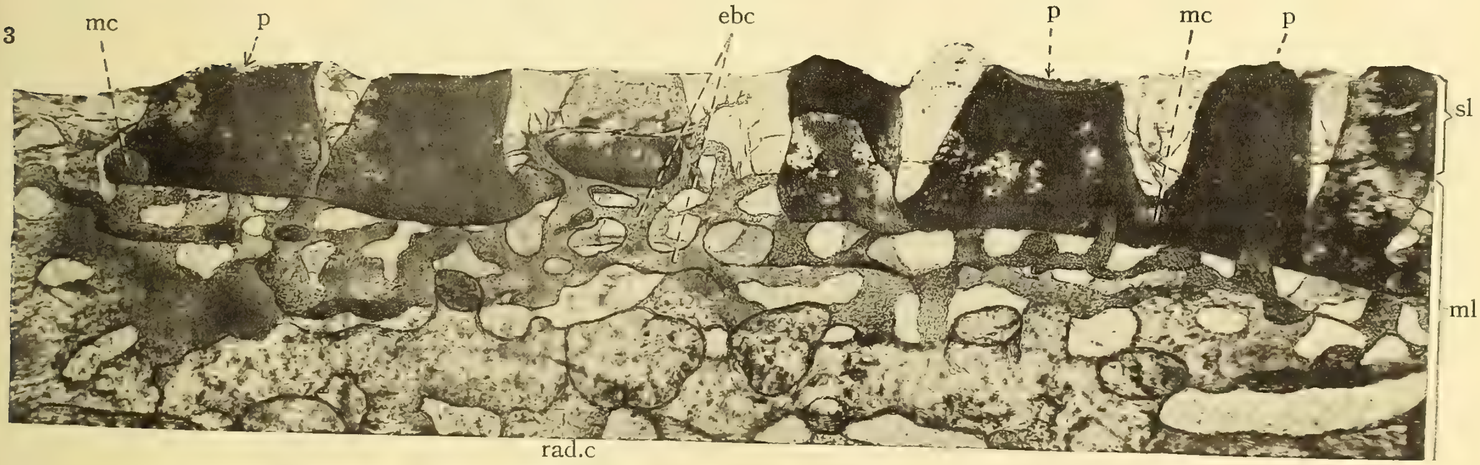

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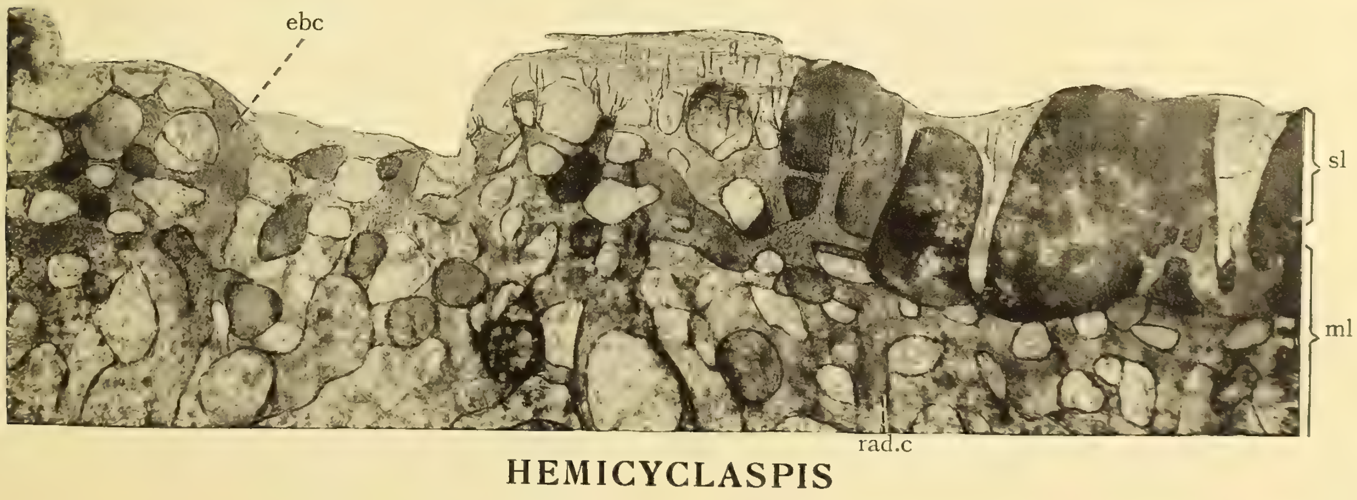


HEMICYCLASPIS

BRITISH
MUSEUM

1 DEC 52

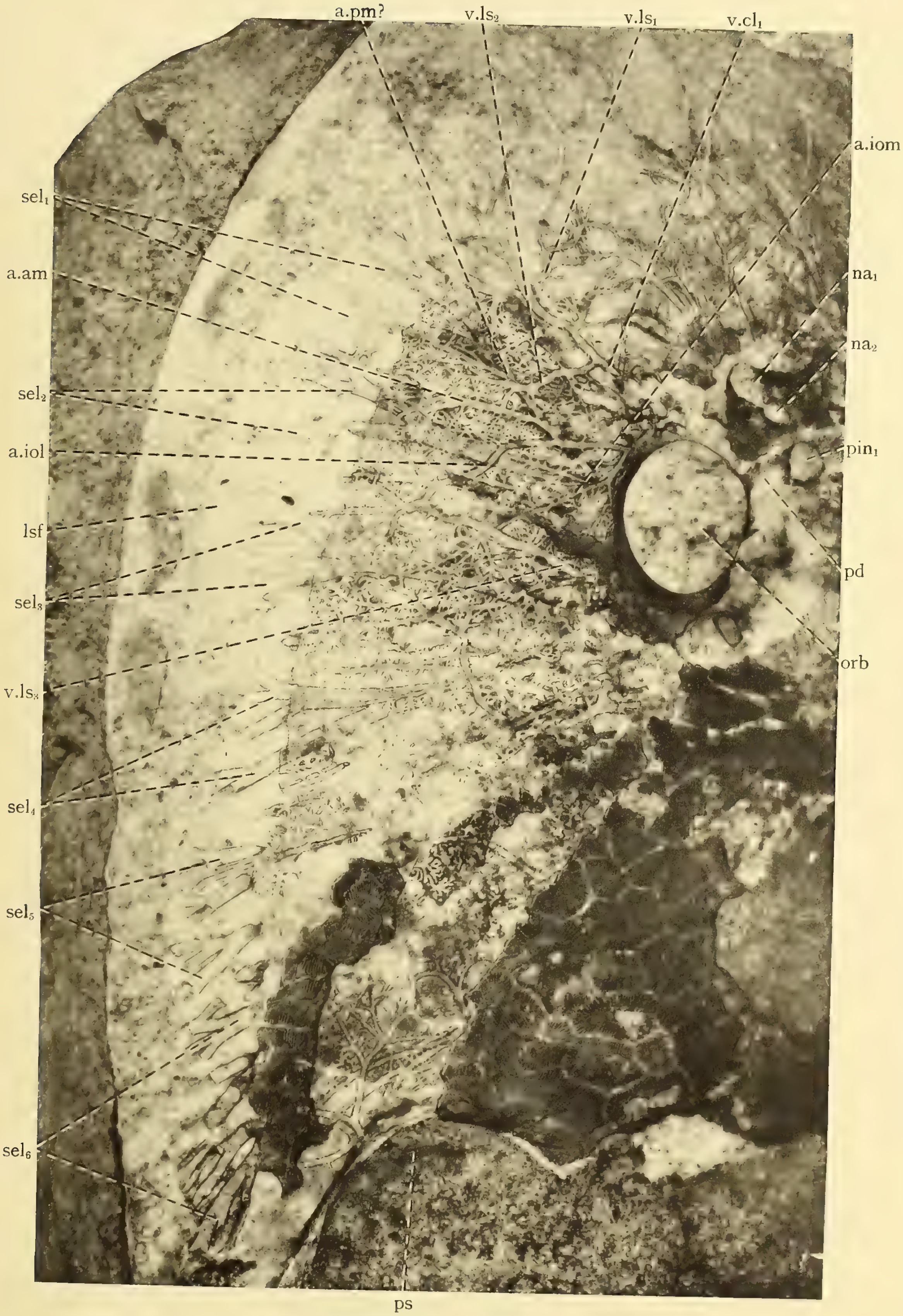
NATURAL
HISTORY.

PLATES 61, 62.

Cephalaspis whitei, sp. nov.

Vascular canals of sub-aponeurotic (sub-cutaneous) vascular plexus of dorsal side of cephalic shield. Pl. 61, left half of dorsal side; Pl. 62, right half of dorsal side. The bone-tissue was made transparent by means of xylol. (Same specimen as in Pl. 18, fig. 3.)

a.am, canal of mandibular branch of a. facialis; *a.fa,* anterior branch of canal of a. facialis; *a.fac,* canal of a. facialis; *a.iol,* lateral infra-orbital branch of canal of a. facialis; *a.iom,* medial infra-orbital branch of canal of a. facialis; *a.pm*?, supposed pre-mandibular branch of canal of a. facialis; *a.sa, a.sm*$_1$, canals of dorso-lateral superficial arteries 1 and 2; *dsf,* dorsal electric field; *lsf,* lateral electric field; *na*$_1$, anterior division of naso-hypophysial aperture (external opening of hypophysial sac); *na*$_2$, posterior division of naso-hypophysial aperture (nasal opening proper); *orb,* orbital opening; *pd,* pineal depression; *pin*$_1$, pineal opening on dorsal side of endoskeleton of cephalic shield; *ps,* pectoral sinus; *sel*$_1$–*sel*$_6$, canals of nerves 1–6 of lateral electric field; *v.cl*$_1$, canal of pre-orbital division of v. capitis lateralis; *v.ls*$_1$–*v.ls*$_5$, canals of dorso-lateral superficial veins 1–5; *v.ls*$_6$?, canal, probably for dorso-lateral superficial vein 6.



CEPHALASPIS

BRITISH
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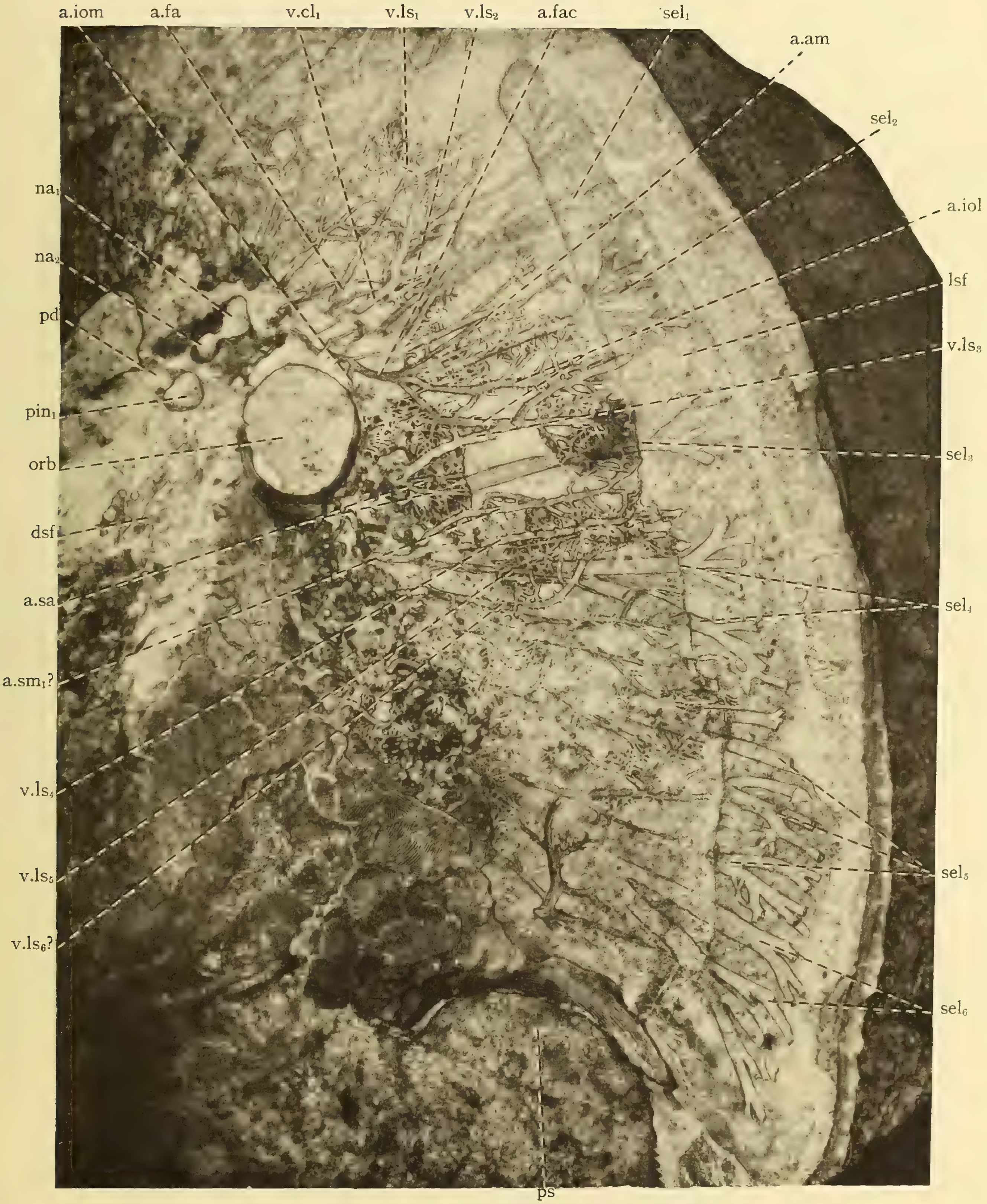
NATURAL
HISTORY.

PLATE 62.

(See Explanation of Pl. 61.)



CEPHALASPIS

BRITISH
MUSEUM
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NATURAL
HISTORY

PLATE 63.

Cephalaspis salweyi Egerton.

Fig. 1.—Section through basal layer of dorsal exoskeleton, showing resorption phenomena, especially around the ascending vascular canals. Lower Old Red Sandstone: loc. unknown. Naturhistoriska Riksmuseum, Stockholm [not numbered]. × 65 diam.

Hemicyclaspis (?) *lightbodii* (Lankester).

Fig. 2.—Section through part of exoskeleton of dorsal side of cephalic shield. Downtonian: loc. unknown. Hereford Museum [not numbered]. Approx. × 55 diam.

Fig. 3.—Part of same, more highly magnified. Approx. × 115 diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals; *ebc*, external branches of radiating canals; *ml*, middle layer of exoskeleton; *rad.c*, radiating canals; *sl*, superficial layer of exoskeleton.

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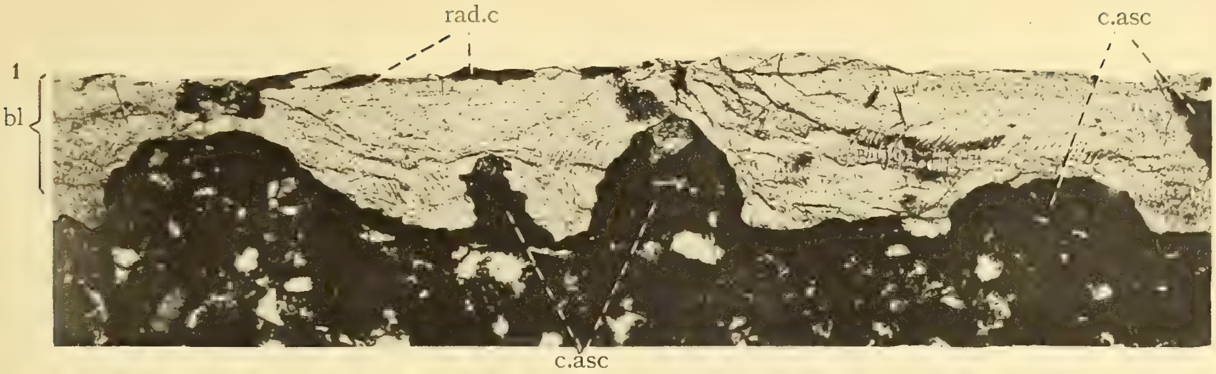

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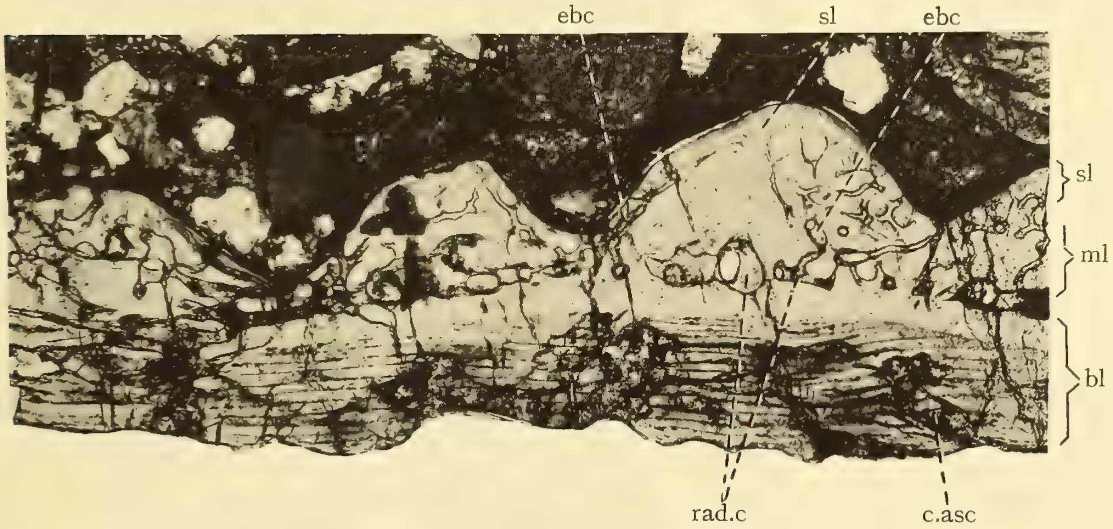

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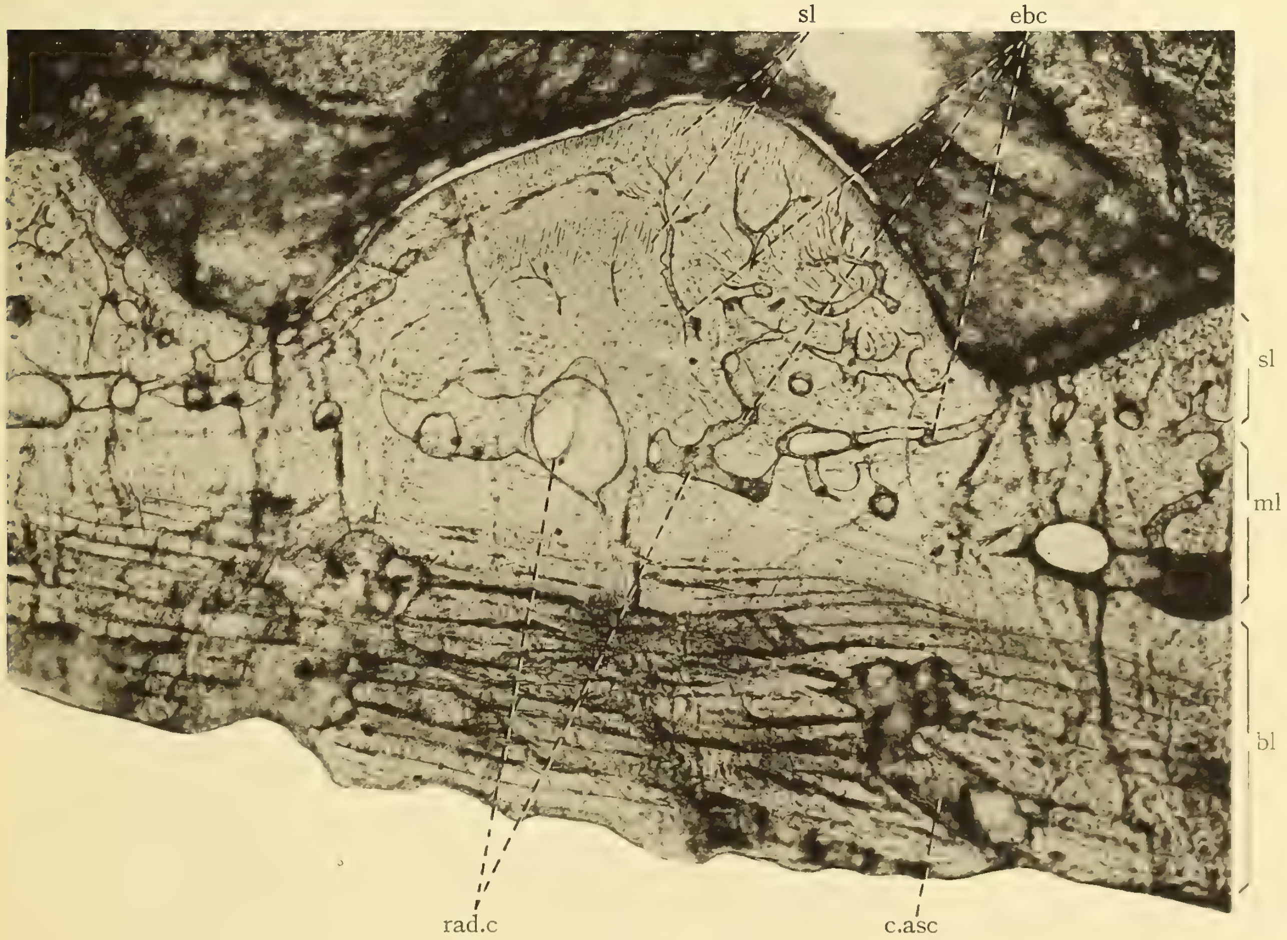

HEMICYCLASPIS

BRITISH
MUSEUM
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NATURAL
HISTORY.

PLATE 64.

Hemicyclaspis murchisoni (Egerton).

FIG. 1.—Section through rostral part of cephalic shield showing dorsal exoskeleton of shield above and ventral exoskeleton of shield (ventral rim) below; the latter, however, is in a poor state of preservation. (From same specimen as Pl. 60: see also Pl. 65, fig. 1.) × 55 diam.

Cephalaspis sp.

FIG. 2.—Section through dorsal exoskeleton of cephalic shield. The superficial layer forms here a continuous covering to the middle layer. (Same specimen as in Pl. 45, fig. 3; see also Pl. 59, fig. 3.) × 55 diam.

FIG. 3.—Part of same, more highly magnified to show the details of the relations between the mucous canal system and the underlying vascular canals. × 200 diam.

bl, basal layer of exoskeleton; *dplx*, canals of sub-aponeurotic vascular plexus; *ebc*, external branches of radiating canals; *iac*, inter-areal mucous canals; *ita*, intra-areal mucous canals; *mc*, mucous canals in general; *ml*, middle layer of exoskeleton; *p*, pores of mucous canals; *rad.c*, radiating canals; *sl*, superficial layer of exoskeleton.

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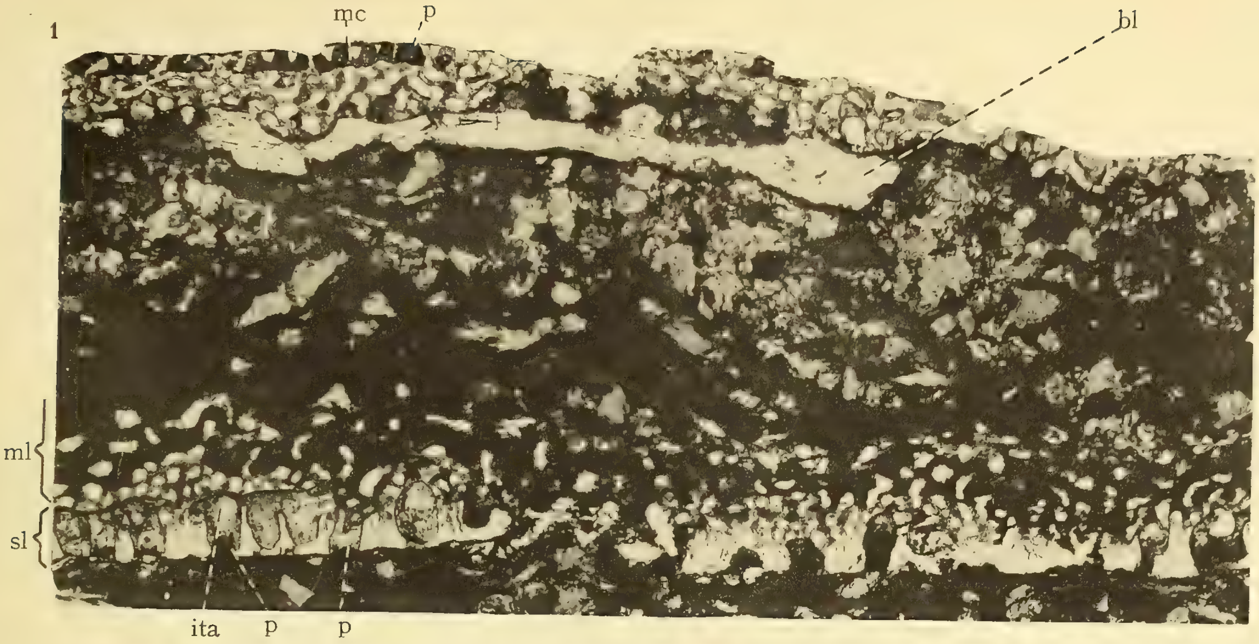

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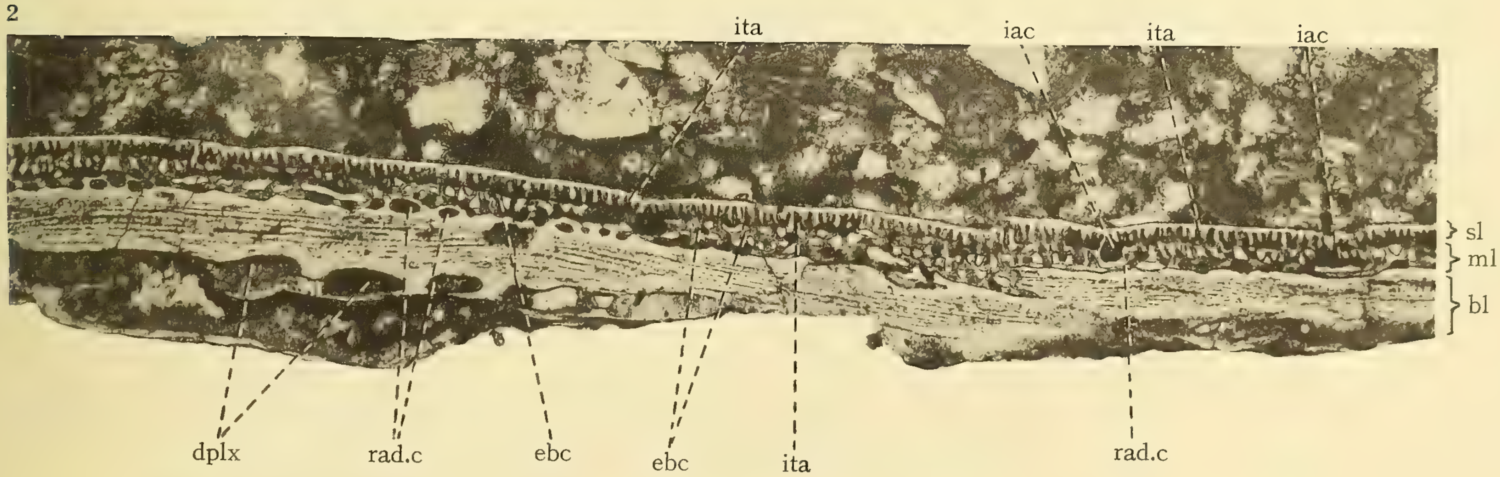

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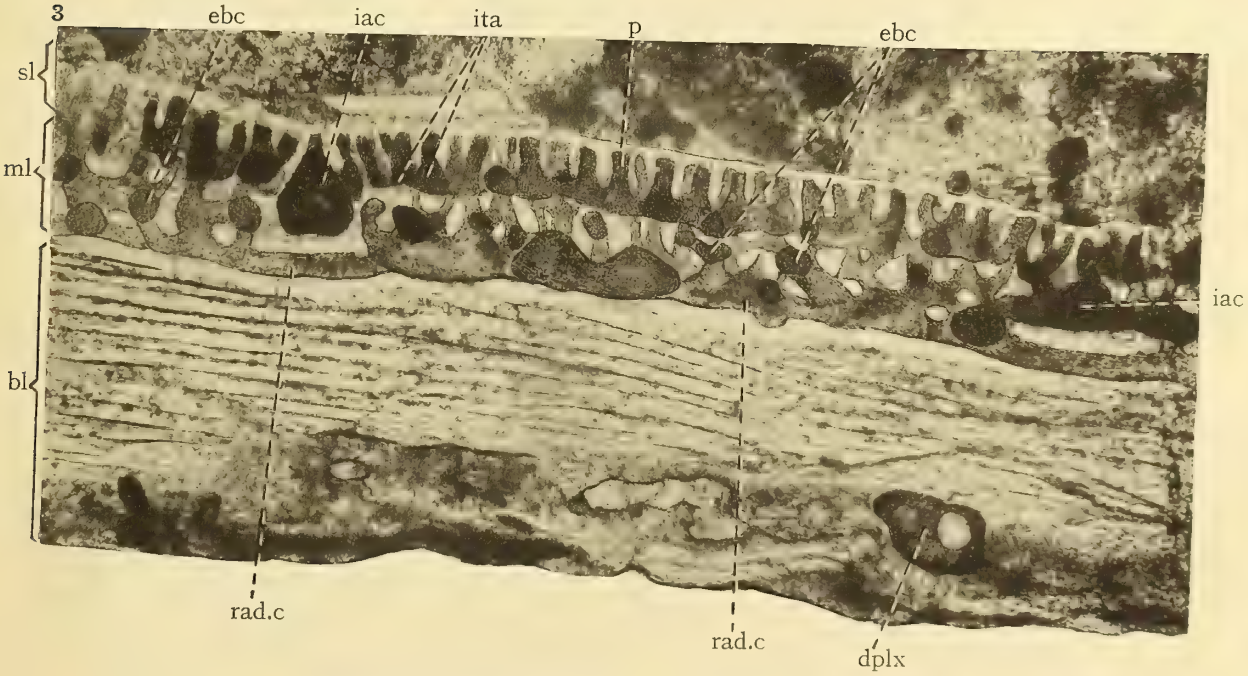

HEMICYCLASPIS and CEPHALASPIS

BRITISH
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NATURAL
HISTORY.

II

PLATE 65.

Hemicyclaspis murchisoni (Egerton).

Fig. 1.—Transverse section through exoskeleton of cephalic shield, approximately midway between rostral margin and orbits. The basal layer shows very clearly resorption phenomena, especially in the sides of the ascending vascular canals. (From same specimen as Pl. 60; see also Pl. 64, fig. 1.) × 115 diam.

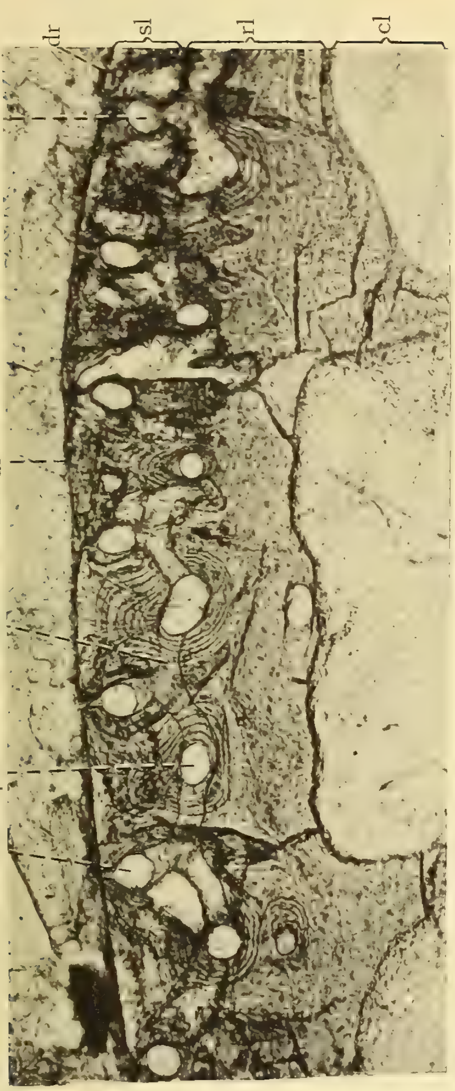
Fig. 2.—Middle portions of lateral scales made transparent by means of oleum cedri in order to show the mucous canal system; external view. (From part of same specimen as Pl. 5, fig. 6; see also Pl. 8, fig. 3.) Approx. × 15 diam.

Fig. 3.—Same specimen and similarly treated, but showing dorsal ends of lateral scales with parts of adjacent dorso-lateral scales. Approx. × 15 diam.

Pteraspid or Palaeaspid.

Fig. 4.—Transverse section through outer parts of exoskeleton, showing position of mucous grooves (*mc*) and vascular canal (*ebc*) leading to them. Downtonian: Spitsbergen. Naturhistoriska Riksmuseum, Stockholm [not numbered]. × 175 diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals; *cl*, cancellous layer of exoskeleton; *dls*, dorso-lateral scales; *dr*, dentine-ridges; *ebc*, canals corresponding to external branches of radiating canals of Cephalaspids; *ls*, lateral scales; *mc*, mucous canals (in fig. 4, mucous grooves); *ml*, middle layer of exoskeleton; *pu*, pulp-like cavity of dentine-ridges; *rad.c*, radiating canals; *rl*, erticular layer of exoskeleton; *r.sin*, venous ring-sinus; *sl*, superficial layer of exoskeleton.



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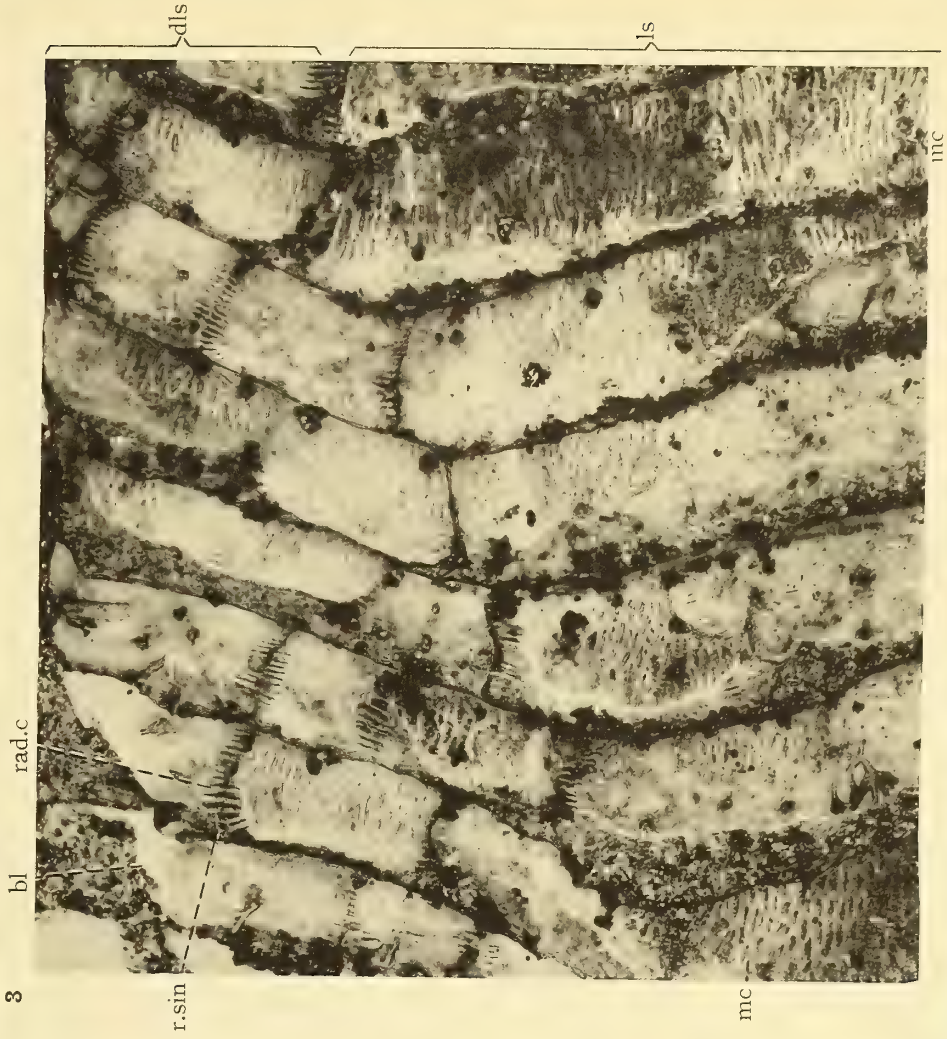

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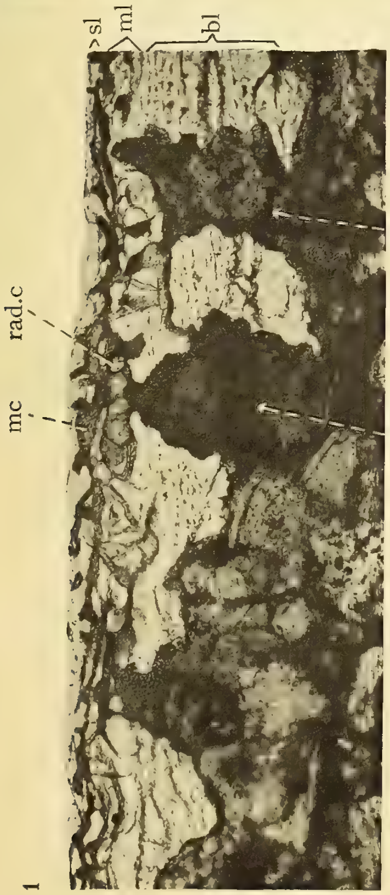

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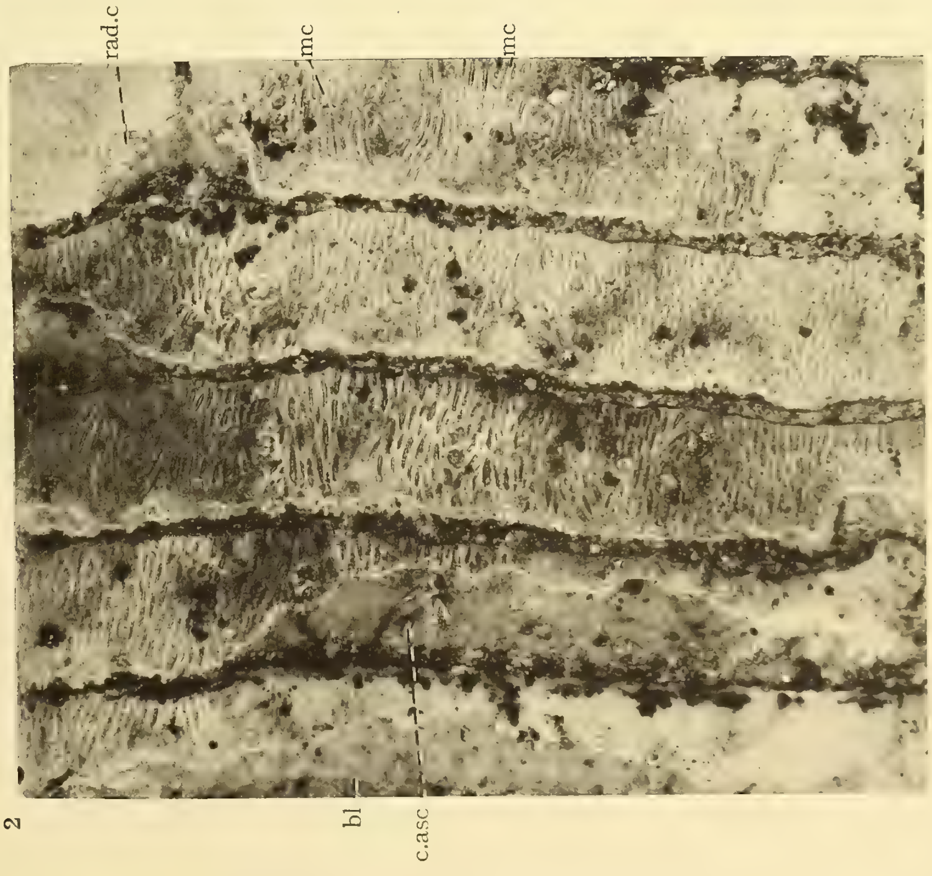

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CEPHALASPIS, HEMICYCLASPIS, Etc.

BRITISH
MUSEUM
1 DEC 32
NATURAL
HISTORY.

PLATE 66.

Cephalaspis salweyi Egerton.

FIG. 1.—Transverse section through exoskeleton of cephalic shield. The basal layer is normally developed, but indications of resorption phenomena are nevertheless to be seen around the ascending vascular canals. (From counterpart of specimen in Pl. 12, fig. 2.) British Museum [no. **P. 191.**—Weaver Jones Coll., 1880]. × 105 diam.

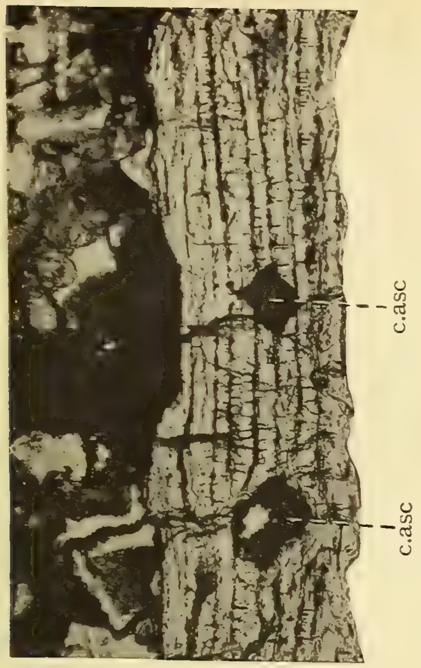
FIG. 2.—Transverse section through basal layer of exoskeleton of cephalic shield. The basal layer is here normally developed. Lower Old Red Sandstone: Cradley, Herefordshire. Royal Scottish Museum, Edinburgh [no. **1891.92.178.**—J. Powrie Coll.]. × 80 diam.

FIGS. 3, 4.—Transverse sections through basal layer of cephalic shield. The under-surface of the layer faces downwards in both figures. The basal layer here shows very distinct resorption phenomena around the grooves of the venous ring-sinuses. Lower Old Red Sandstone: loc. unknown. British Museum [no. **35499.**—Purchased, 1860]. × 80 diam.

Psammosteus arenatus Agassiz.

FIGS. 5, 6.—Sections through superficial parts of exoskeleton from specimen doubtfully referred to this species. Upper Devonian: Spitsbergen. Naturhistoriska Riksmuseum, Stockholm [not numbered]. × 55 diam.

bl, basal layer of exoskeleton; *c.asc*, ascending vascular canals; *ebc*, external branches of radiating canals; *mc*, mucous grooves; *ml*, middle layer of exoskeleton; *rad.c*, radiating canals; *r.sin*?, supposed groove of venous ring-sinus; *sl*, superficial layer of exoskeleton.



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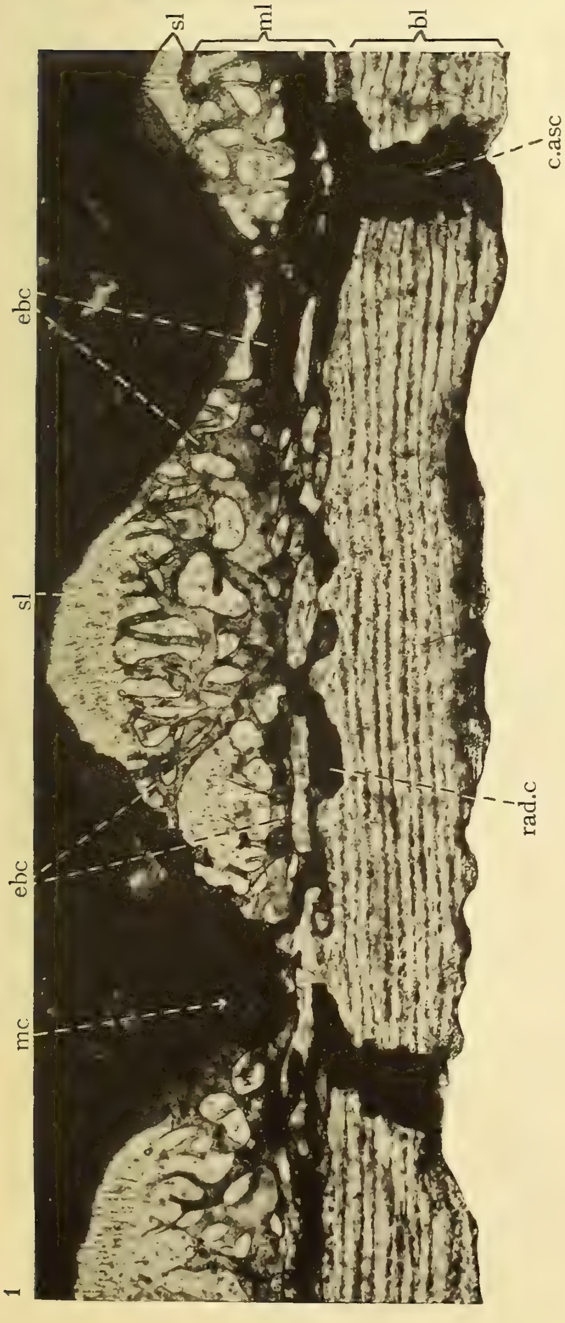

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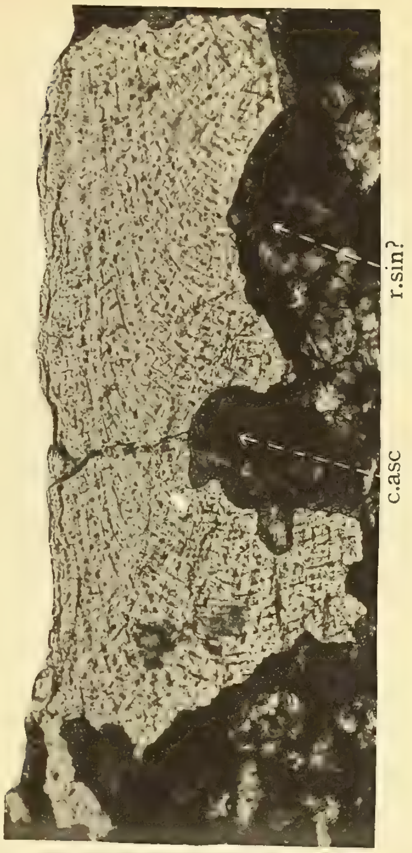

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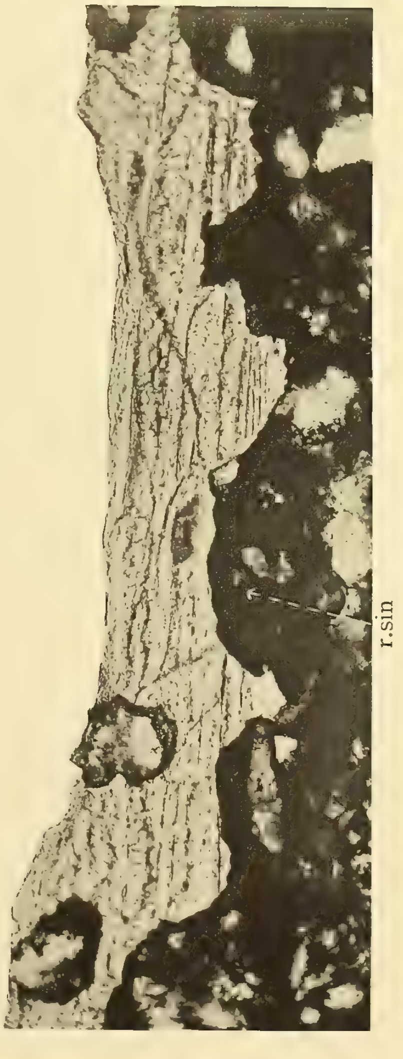

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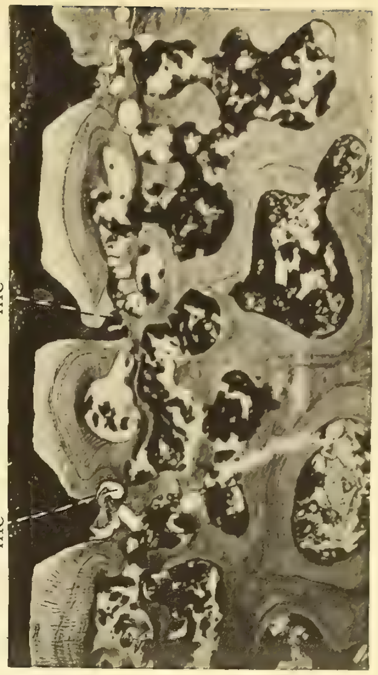

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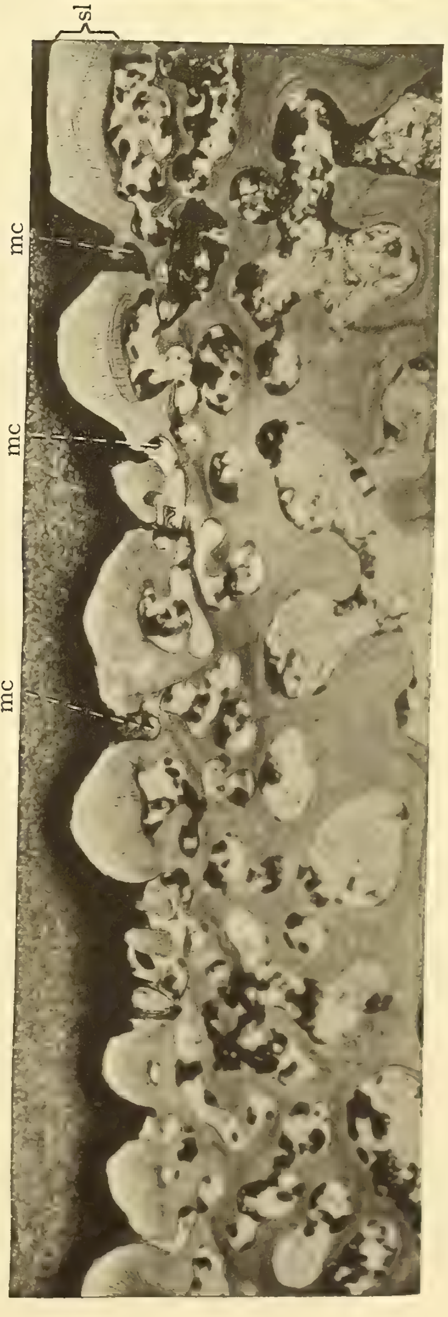

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CEPHALASPIS and PSAMMOSTEUS

BRITISH
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